Which features of protected areas make them attractive to wildlife-based tourists?

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Global Wildlife-Based Tourism

Which features of protected areas make them attractive to wildlife-based tourists?

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List of Abbreviations

GLM	Generalised Linear Model
IOA	Index of Attractiveness
IUCN	International Union for the Conservation of Nature
LOS	Likelihood of Selection
NB	Nature-based
NBT	Nature-based Tourism
PA	Protected Area
TM	Terrestrial Mammal
WB	Wildlife-based
WBT	Wildlife-based Tourism
WDPA	World Database of Protected Areas

Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University, or any other University. The research reported within this thesis has been conducted by the author, unless indicated otherwise.

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This thesis is written and analysed wholly by myself, unless referenced. However, the production of this work could not have happened without the support and guidance of my supervisors, colleagues, friends and family.

Errata for MSc Thesis

Harriet Newhouse

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Subsequent to producing this thesis, errors were detected in the compilation of some of the data used in analyses, which may have materially affected inference. It became apparent that misclassifications had occurred in the collated data. For example, Iberian Lynx were found to be associated with Russian protected areas (PAs), Africa Elephant were found to be associated with Indian PAs and all sloth records across South America were found to be associated with a single, rare island-endemic species. These misclassifications will have affect the attractiveness values allocated to each terrestrial mammal species in Chapter 2 and the assemblage attractiveness values allocated to each PA in Chapter 3.

Abstract

Wildlife-based tourism (WBT), defined as any form of tourism that is based on visitors encountering wildlife (Higginbottom & Tribe 2005), is capable of generating substantial revenue for both local economies and conservation (Dharmaratne *et al*. 2000; Lindsey *et al*. 2007; Bayliss *et al*. 2014). It is largely based in protected areas (PAs) and provides important justification for their continued existence, as they come under increasing pressure for land to be put to alternative, not conservation uses, such as agriculture and mining (Balmford *et al.* 2015). Yet, the principal factors that drive wildlife-based (WB) tourists to visit specific PAs remain poorly understood. In this thesis, I explored the (1) species traits and (2) features of PAs that make them attractive to WB-tourists. In Chapter Two, I built a modelling framework to predict terrestrial mammal (TM) species attractiveness, based on a range of species traits and characteristics. The model predicted that large, increasingly threatened TM species are more attractive to WB-tourists than smaller, more common TM species. In Chapter Three, I built a modelling framework to predict PA attractiveness, based on a range of socioeconomic and biogeographical variables. The model predicted that larger, less remote PAs, with higher wildlife attractiveness values, are more attractive to WB-tourists than smaller, more remote PAs, with lower wildlife attractiveness values. I used the model to highlight PAs with high WBT potential that are currently underexploited. The model highlighted PAs in upper Amazonia and sub-Saharan Africa. New WBT operations in these regions could have significant socioeconomic benefits for local communities, could help generate substantial revenue for conservation and help prevent the over-utilisation of 'popular' WBT sites that have already been heavily exploited. However, tour operators must strike a balance between satisfying tourist demand and minimising the stress and disturbance caused to the environment by WB-tourists, to ensure WBT has a net positive impact on PA biota (Lindsey *et al*. 2007; Bayliss *et al*. 2014).

Chapter One: Introduction

1.1 Global Reduction in Biodiversity

Analogous to hospital triage, conservation biology has been described as a crisis discipline; the list of species at imminent risk of extinction is continuously growing (Bottrill *et al.* 2008), conservation budgets are limited (Myers *et al.* 2000), and decisions need to be made rapidly, regarding which species to save (Wilson & Tisdell 2001). Threats to global biodiversity, such as habitat loss and degradation, invasive species, overexploitation and climate change, are increasing, whilst most indicators of the state of global biodiversity, including population sizes, habitat extents and community compositions, are in decline (Butchart *et al*. 2010). It has been predicted that over 30% of species will be committed to extinction by 2050 (Thomas *et al*. 2004; Watson *et al*. 2016). Loss of biodiversity has caused widespread concern for both ethical and aesthetic reasons (Hooper *et al*. 2005), but also for ecosystem functioning (Schwartz *et al.* 2000). Ecosystem functioning includes the goods and services ecosystems provide to humanity (Christensen *et al.* 1996). Ecosystem goods have direct market value, such as food, construction materials and medicines, whilst ecosystem services are properties of ecosystems that have direct, or indirect, benefits to humans, such as regulating climate, cleansing water, cycling of nutrients and tourism (Costanza *et al.* 1997). It has been estimated that, as global biodiversity declines, approximately $US4.3-20.2 trillion worth of land-based ecosystem services are being lost every year (Costanza *et al.* 2014). One study found that the amount of funding a threatened species receives is strongly correlated with its chance of making a successful recovery, suggesting that the rate of species extinctions could be reduced by legalising and utilising all possible sources of revenue for conservation (Gerber 2016). However, this study was based on data from the USA and it remains untested whether such strong correlations are found more broadly.

1.2 Global Mass Tourism

Global mass tourism is a key driver of economic growth and development, and is one of the fastest-growing industries in the world (UNWTO 2015). It contributes 9% of global gross domestic product (GDP) and boasts an annual economic impact of around US$6.5 trillion per year, with expected growth to US$10 trillion by 2022 (Seddighi & Theocharous 2002). In 2014, the number of international tourist arrivals worldwide exceeded 1.1 billion; this figure is forecast to increase annually by 3.3% until 2030, when it is due to reach 1.8 billion (UNWTO 2015). Tourism is also responsible for the creation of sustainable enterprises and jobs, providing millions of people worldwide with greater stability and overall quality of life (UNWTO 2015). In the Caribbean, for example, 17% of the available workforce is employed in the tourism sector (Carr & Heyman 2009).

1.3 Nature-Based Tourism

Nature-based tourism (NBT) is any form of tourism that relies on experiences directly related to natural attractions (Balmford *et al.* 2009). It includes wildlife-based tourism (WBT) and ecotourism, as well as aspects of rural tourism, 'consumptive uses of wildlife' and 'human relations with animals' (Figure 1.1). WBT is any form of tourism that is based on visitors encountering wildlife (Higginbottom *et al*. 2005), whilst ecotourism is defined as "*responsible travel to natural areas that conserves the environment and improves the well-being of local people*" (TIES 2000). 'Consumptive use of wildlife', within the context of NBT, includes activities such as hunting and fishing, and involves animals being deliberately killed or having body parts utilised (Freese 1998). Rural tourism is typically concerned with broader issues of regional development in a farmed landscape, whilst 'human relations with animals' includes

the role of pets as therapy, animal rights and husbandry, as well as aspects of wildlife management (Reynolds & Braithwaite 2001).

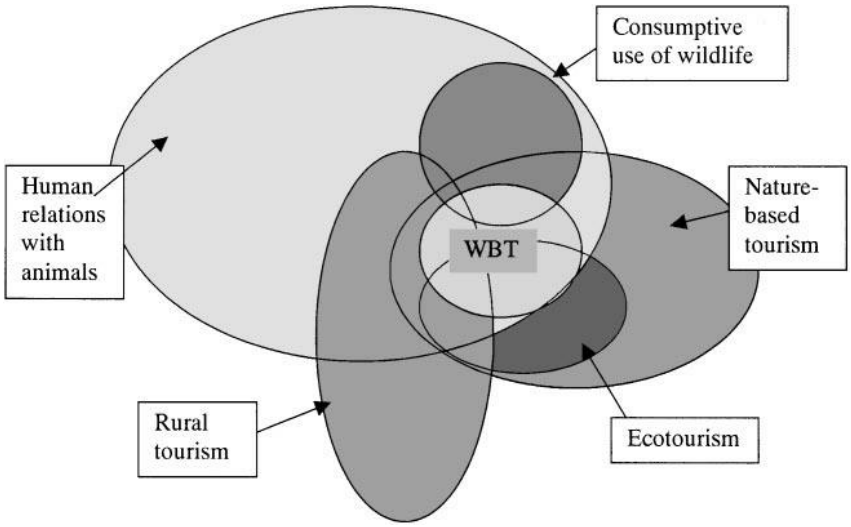


Figure 1.1: Relationship between different forms of nature-based tourism (Reynolds & Braithwaite 2001).

NBT generates approximately US$600 billion per year, in direct in-country expenditure (Balmford *et al.* 2015), and is now recognised as the most prominent cultural ecosystem service; these are defined as ecosystem services that benefit humans through 'spiritual enrichment, cognitive development, recreation and/or aesthetic experiences' (Bateman *et al.* 2011). NBT operations in the Galapagos contribute more than US$100 million to the local economy each year (Thirgood *et al*. 2006), meanwhile, in South Africa NBT generates approximately the same revenue as farming, forestry and fisheries combined (TIES 2000). The dependence of NBT on natural ecosystems can help motivate and incentivise tour operators and host communities, who benefit financially from NBT, to conserve wildlife species and/or the habitats in which they reside (Buckley 2000; van Oosterzee 2000; Sekercioglu 2002). In a survey of 27 private game-reserve managers in South Africa, 48% said that if NBT had not been a commercial option, they would have continued to farm cattle, which is generally considered to be a less sustainable land-use in such areas (James & Goodman 2000).

1.4 Protected Areas

Protected areas (PAs) are defined by the International Union for the Conservation of Nature (IUCN) as: *"clearly defined geographical spaces, recognised, dedicated and managed, through legal or other effective means, to achieve the long term conservation of nature, with associated ecosystem services and cultural value"* (Dudley 2008). PAs now represent one of the most significant forms of human land use, covering more than 15% of the Earth's land area (UNEP-WCMC 2014), and are commonly recognised as the most important unit for *in situ* conservation (Chape 2005). *In-situ* conservation, defined as "*the conservation of ecosystems and natural habitats, and the maintenance and recovery of viable populations of species, in their natural surroundings*" (CBD 1992), is generally more secure, and financially efficient, than *ex-situ* methods of conservation (Gaston *et al*. 2008). Viable populations of some species can be maintained *ex-situ,* however, we lack the knowledge and resources required to successfully conserve all species in captivity (Cairns 1987). PAs also host the majority of NBT activities worldwide, receiving approximately 8 billion visits from nature-based tourists each year (Balmford *et al.* 2015). Despite their dual purpose in biodiversity conservation and human recreation, PAs are under increasing pressure for land to be put to alternative, non-conservation uses, such as: mining, logging and agriculture (Dodd *et al.* 2012; Goodwin *et al*. 1998). With the ongoing threat of local extinctions, biodiversity loss and species declines (Suhkdev 2009; Butchart *et al.* 2010), it is becoming increasingly important to consider whether (or not) the existence of PAs are stemming loss in biodiversity and the value of PAs, in terms of ecosystem service provision (Balmford *et al.* 2015). This latter consideration is especially important if ecosystem services, such as NBT, are expected to 'pay their way' to justify the continued existence of PAs (Chivian & Bernstein 2004; Naidoo & Adamowicz 2005).

1.4.1 Do Protected Areas Help Retain Biodiversity?

Ideally, the impact of PAs on loss of biodiversity would be assessed by comparing the overall biodiversity of each PA with what would have happened in the absence of protection (Bernard *et al.* 2014). However, this comparison cannot be readily achieved. Instead, previous studies have compared biodiversity inside PAs with that of surrounding, unprotected areas (Coetzee *et al.* 2014; Caro 2002; Edgar *et al.* 2004; Ashworth & Ormond 2005; Naughton-Treves *et al.* 2005; Micheli *et al.* 2005; Guidetti 2006; Monaco *et al.* 2007; Friedlander *et al*. 2007; Laurance *et al*. 2011; Gardner *et al*. 2007; Caro *et al*. 2009). The results from these studies have been highly variable. Some report greater richness and/or abundance of species within, compared to outside, PAs (Ashworth & Ormond 2005; Naughton-Treves *et al.* 2005; Micheli *et al.* 2005; Friedlander *et al*. 2007), suggesting that PAs help remove, or reduce, processes that threaten biodiversity (Dinerstein *et al.* 2007; Meijaard & Nijman 2000; Russ & Alcala 2003; Bernard *et al.* 2014; Devictor *et al.* 2007; Gaston *et al.* 2006). Others suggest the converse is true; that the richness and/or abundance of species is greater outside, rather than within, PAs (Caro 2002; Edgar *et al.* 2004; Guidetti 2006; Monaco *et al.* 2007). PAs considered by the former may have been originally designated in regions of greater richness and/or abundance, whilst PAs studied by the latter may have been originally designated in regions of lower richness and/or abundance, than surrounding, unprotected areas (Ashworth & Ormond 2005; Rannestad *et al.* 2006). Although the results of these studies have been variable, recent meta-analyses of such studies suggest that the majority of PAs contain higher abundances of individual species, and higher species richness values, than surrounding, unprotected areas, concluding that PAs do play an important role in stemming loss in biodiversity (Gray *et al.* 2016; Bernard *et al.* 2014).

1.4.2 Benefits of Recreation in Protected Areas

Recreation in PAs is capable of generating substantial revenue for both local economies and conservation (Dharmaratne *et al*. 2000; Lindsey *et al*. 2007; Bayliss *et al*. 2014) and has positive impacts on human health and wellbeing (Chape *et al*. 2005; Hunter *et al.* 2015; Dadvand *et al.* 2015; Cohen-Cline *et al.* 2015). Several studies have shown that participation in 'green exercise', defined as physical activity in the presence of nature, has significant benefits to humans, including greater mental health and immune system functioning i.e. experiencing nature makes us 'happier and healthier people' (Kahn & Kellert 2002; Zaradic & Pergams 2007; Balmford *et al.* 2009; Barton & Petty 2010; Chape *et al*. 2005; Hunter *et al.* 2015; Dadvand *et al.* 2015; Cohen-Cline *et al.* 2015; Lee & Maheswaran 2010; Russel 2013; Bowler *et al.* 2010; White *et al.* 2013). However, the negative impacts of recreation in PAs, specifically the impacts of nature-based tourists on wildlife, can also be significant (Skira & Smith 1991; Orams 1997; Wilson & Stanley 1994; Johnson 1995; Platt 1995; Ringwood & Wesley 1995; Moore *et al.* 1997; Reynolds & Braithwaite 2001; Green & Higginbottom 2001; Béchet *et al.* 2004; Stelios & Melisidou 2007; Stronza & Pegas 2008; Naylor *et al.* 2009; Ciuti *et al.* 2012).

1.5 Negative Impacts of Nature-Based Tourism

Construction of accommodation, road infrastructure, parking spaces and picnic areas for tourists often requires the removal, or modification, of habitat (Green & Higginbottom 2001). This may reduce the size of an animal's territory or home range, improve access for predators or competitors of native species and/or increase wildlife emigration, which is a prelude to mortality (Butynski & Kalina 1998). Increased road traffic in wildlife-rich areas, due to higher numbers of tourist vehicles, can increase the rate of wildlife mortality caused by collisions (Reynolds & Braithwaite 2001; Green

& Higginbottom 2001) and increase the rate of juvenile mortality as tourist vehicles sometimes separate parents from their offspring (Edington & Edington 1990).

Presence of tourists can reduce the time animals spend feeding (Naylor *et al.* 2009; Ciuti *et al.* 2012), and increase their energy expenditure from perceived danger (Béchet *et al.* 2004). This can lead to a deterioration of animal condition and subsequent decline in reproductive success, as resources are usually only allocated to breeding when animals are in good condition (Isaacs 2000; Béchet *et al.* 2004; Stronza & Pegas 2008). Presence of tourists can also interfere with provisioning of offspring and/or increase the rates of offspring predation, either by inadvertently advertising the locations of breeding sites, or by distracting adults from defending their young (Ellison & Cleary 1978; Anderson & Keith 1980).

Exposing wildlife to novel stimuli produced by tourists, such as frequencies and intensities of sound not otherwise encountered in their natural environments, can detrimentally influence the responses of wildlife (Bowles 1995). Nocturnal mammals, for example, often rely on their sensitive hearing for prey detection (Bowles 1995). Low-frequency noise pollution can induce vibrations, which may confuse the signals needed when hunting prey (Bowles 1995). Furthermore, hand-feeding of wildlife is becoming increasingly common, however, intentional feeding of wildlife by tourists can contribute to an imbalanced diet, decreasing the vitality and survival of animals (Orams 2002). Petting and handling of wildlife, when not managed appropriately, can cause stress to animals (Van Tiggelen 1994), which can result in weight loss, reduced breeding success and increased vulnerability to disease (Siegel 1980). This latter point is of particular concern as disease transmission from tourists to wildlife is a serious threat, especially to endangered populations of apes (Skira & Smith 1991; Orams 1997; Wilson & Stanley 1994; Johnson 1995; Platt 1995; Ringwood & Wesley 1995, Moore *et al.* 1997). In addition, hand-feeding by tourists can encourage wildlife

to spend more time around roads and other tourist facilities, which further increases the likelihood of collision with vehicles (Skira & Smith 1991).

Tourists can also have negative sociocultural impacts on host communities, threatening indigenous identities, local cultures and religious traditions, by introducing new behaviours and value systems (INTOSAI 2015). Tourists increase the demand on basic goods and services, as well as on local real estate (Stelios & Melisidou 2007). This often results in increased prices, which can exclude local residents whose incomes do not increase proportionally (Stelios & Melisidou 2007). Furthermore, developers often demand improved transport links and infrastructure for tourists, which can place financial pressure on local governments and taxpayers, frequently resulting in funding cuts in other sectors, such as health and education (Stelios & Melisidou 2007).

1.6 Ecotourism

Ecotourism is the fastest growing component of the tourism industry, growing at a rate almost three times faster than global mass tourism (Gössling *et al.* 2002; Blangy & Mehta 2006). Ecotourism currently constitutes more than 7% of global tourism demand, accounting for approximately US$100 billion per year (Centre for Responsible Travel 2011). The global significance of ecotourism was confirmed when the World Ecotourism Summit attracted over 1000 delegates, from 132 countries (TIES 2010). Ecotourism follows a distinct set of principles and good practices, aiming to minimise the negative impacts of tourism, and instead make positive contributions to a number of today's environmental and social challenges (Stronza & Pegas 2008).

The three main objectives of ecotourism are to: (1) protect and enhance the environment, minimising the negative environmental, economic and social impacts often associated with tourism, (2) educate tourists at the natural site, and (3) respect local cultures and improve the livelihoods of local people (Wunder 2000; Blangy & Mehta 2006; Stronza & Pegas 2008).

1.6.1 Minimising Negative Impacts of Tourism

The International Ecotourism Society (TIES) believe that, whilst the negative impacts of tourism cannot be completely eliminated (Reynolds & Braithwaite 2001), they can be minimised using established frameworks that emphasise proper planning and wildlife management, before and during development, as well as parallel to the running of new ecotourism projects (Kruger 2005; Blangy & Mehta 2006). TIES have a Certification Program which serves as a tool for distinguishing genuinely responsible companies, products or services from those that use descriptors, such as 'eco' and 'sustainable' as marketing tools to attract consumers (TIES 2010). TIES also provide guidelines and ecological specifications for ecotourism infrastructures (Blangy & Mehta 2006). For example, specifying that eco-lodge sites should be situated "*just outside the nature reserve, in less sensitive areas, preferably in previously disturbed sites and where the lodge would not directly after the flagship ecotourism attraction*" (TIES 2010).

Honeypot sites are used to help reduce the impacts of tourists on wildlife (Stronza & Pegas 2008). They attract tourists, yet keep them away from vulnerable conservation areas (Warren 1997). For example, the CairnGorm funicular railway in Scotland allows visitors to reach the top of the CairnGorm Mountain (the honeypot site). However, as passengers are not permitted to exit the top station to go onto the mountain (unless they are booked on a guided walk or guided mountain bike descent)

the impact of tourists on the vulnerable wildlife of the CairnGorm Mountain has been reduced (Warren 2002). Other management strategies, used to reduce the negative impacts of tourists on wildlife, include: seasonal closures, zoning of activities, restrictions on equipment (such as bans on motorised vehicles, guns and/or fires), as well as restrictions on group sizes, lengths of stays and/or daily visitor numbers to PAs (Stronza & Pegas 2008; Giongo *et al.* 1993). For example, regulations for western gorilla (*Gorilla gorilla*) watching, in Volcanoes National Park, Rwanda, include a maximum group size of eight tourists, for a maximum of one hour, to any single gorilla group, per day (Stronza & Pegas 2008).

1.6.2 Education of Ecotourists

Some studies report relatively weak links between increased knowledge and behavioural change (Reddy *et al.* 2016), whilst other studies suggest that education helps generate important support for conservation, promotes more responsible behaviour of tourists towards wildlife and the natural environment, encourages involvement of tourists in wildlife conservation and research, and often results in greater voluntary donations for conservation (TIES 2000). Improving public knowledge and concern about the environment can also increase the political pressure on governments to achieve conservation goals (Higginbottom *et al*. 2005).

1.6.3 Local Cultures and Livelihoods

The final objective for ecotourism is to respect local cultures and improve the livelihoods of local people (Wunder 2000). Ecotourism often has greater potential to reduce poverty than other economic development options, as it can be labour-intensive, generating more jobs and income opportunities for local communities, and inexpensive to develop, as it uses existing natural, cultural and historical resources

(Blangy & Mehta 2006). Ecotourism also attracts outside investments in the development of infrastructure, which can serve the needs of both locals and tourists (Blangy & Mehta 2006). However, there are few examples of successful, community-run ecotourism operations, and it is uncertain how much local communities benefit, especially when it comes to wealthy ecotourists who expect luxury goods and services, usually purchased outside the rural economy (Blangy & Mehta 2006). Local residents rarely possess the skill set demanded by ecotourism jobs (for example, knowledge of language beyond the local dialect), or the capital required to start-up businesses in the ecotourism industry (Timothy 2002). Consequently, the benefits of ecotourism are often received by a few local elites, rarely reaching those less fortunate (Coria & Calfucura 2012).

1.7 Wildlife-Based Tourism

WBT is any form of tourism that is centred on visitors encountering wildlife (Reynolds & Braithwaite 2001), and is largely based in PAs (Higginbottom *et al*. 2005). It has been defined as the area of overlap between NBT, ecotourism, 'consumptive use of wildlife', rural tourism and 'human relations with animals' (Figure 1.1). The term 'wildlife' technically covers both flora and fauna, however, within the tourism industry, the definition of 'wildlife' is restricted to fauna (Reynolds & Braithwaite 2001).

This thesis focuses on non-consumptive forms of WBT, specifically tourism that is based on watching free-ranging species in their natural environments (Valentine & Birtles 2006). It does not consider other wildlife-based activities, such as hunting, fishing or viewing captive wildlife in zoos. Wildlife-watching is an observation activity, though it can sometimes involve interactions with the animals being watched (Caudill 2003). It has been estimated that the wildlife-watching industry in North America alone generates approximately US$95.8 billion in total industry output, and over 1

million jobs, each year (Caudill 2003). The introduction of lion (*Panthera leo*) to Pilanesberg National Park, South Africa, was estimated to generate US$9 million through wildlife-watching activities to the regional economy (McNeely 2000). Each individual lion in Amboseli National Park, Kenya is calculated to be worth US$515,000 as a wildlife-watching resource over its lifetime (Thresher 1981). Meanwhile, in Rwanda, western gorillas (*Gorilla gorilla*) generate approximately US$4 million per year, as a wildlife-watching resource (Tapper 2006), accounting for over 75% of Rwanda's tourism income (Shackley 1995).

The principal drivers of WBT, in terms of features of PAs that make them attractive to wildlife-based tourists, remain poorly understood (Luisetti *et al.* 2011; Naidoo *et al.* 2011; Clucas *et al*. 2008; Smith *et al*. 2012; Arponen *et al*. 2014). A greater understanding of these features is required, in order to improve understanding of what drives wildlife-based tourists to specific destinations, and to highlight sites with high WBT potential that are currently under-exploited. This could help generate substantial revenue for both local economies and conservation in the highlighted regions (Dharmaratne *et al*. 2000; Lindsey *et al*. 2007; Bayliss *et al*. 2014); motivate and incentivise tour operators and host communities, who benefit financially from WBT, to conserve the species and/or the habitats in which they reside (Buckley 2000; van Oosterzee 2000; Sekercioglu 2002); and, provide important justification for the continued existence of PAs, as they come under increasing pressure for land to be put to alternative, not conservation uses, such as agriculture or mining (Dodd *et al.* 2012; Goodwin *et al.* 1998).

1.8 Aims and Objectives

This thesis aims to:

(1) Identify the traits that lead to specific species being mentioned more times within wildlife-based tourism guidebooks, travel brochures and online resources

(2) Identify the features of PAs (including the species present) that lead to them being mentioned more times within wildlife-based tourism guidebooks, travel brochures and online resources

1.9 Thesis Plan

In Chapter Two, I explore the traits that make terrestrial mammal (TM) species more attractive to wildlife-based tourists. I build a modelling framework to predict TM species attractiveness, based on species traits and characteristics. The model is used to allocate values of attractiveness to all TM species. I use these values, along with a range of other predictor variables, in Chapter Three to predict PA attractiveness.

In Chapter Three, I explore the factors that lead to specific PAs being popular for WBT. I build a modelling framework to predict PA attractiveness, based on a range of biophysical and socioeconomic variables, and use the model to highlight priority sites for WBT.

Chapter Two: Which traits of terrestrial mammal species make them attractive to wildlife-based tourists?

2.1 INTRODUCTION

Wildlife-based tourism (WBT), defined as any form of tourism that is based on visitors encountering wildlife (Higginbottom *et al*. 2005), is capable of generating substantial revenue for both local economies and conservation (Dharmaratne *et al*. 2000; Lindsey *et al*. 2007; Bayliss *et al*. 2014). WBT is largely based in protected areas (PAs), and is a means of justifying their continued existence as they come under increasing pressure for land to be put to alternative, not conservation uses, such as agriculture or mining (Dodd *et al.* 2012; Goodwin *et al.* 1998). Wildlife is a primary driver of WBT (Higginbottom & Buckley 2003). Yet, there has never been a rigorous, quantitative system to assess the traits that make specific species attractive to wildlife-based (WB) tourists (Luisetti *et al.* 2011; Naidoo *et al.* 2011; Clucas *et al*. 2008; Smith *et al*. 2012; Arponen *et al*. 2014). A greater understanding of these traits is required, in order to improve understanding of what drives WB-tourists to specific PAs.

2.1.1 Wildlife Viewing Preferences

Taxonomy, body mass, rarity and diet have been identified as traits that may be responsible for making specific species attractive to WB-tourists (Krüger 2005; Lindsey *et al*. 2007; Clucas *et al*. 2008; Maciejewski & Kerley 2014; Smith *et al*. 2012; Arponen *et al*. 2014). Previous studies, based on flagship species, suggest that WB-tourists are more attracted to large, rare species, or species that are less frequently encountered, than small, more common species, and are 'thrilled by the act of predation' (Smith *et al*. 2012; Arponen *et al.* 2005). On African game drives, for

example, WB-tourists are reportedly more attracted to African bush elephants (*Loxodonta africana)*, followed by large carnivorous species, such as lion (*Panthera leo*), leopard (*Panthera pardus*) and cheetah (*Acinonyx jubatus*); and that among the herbivores, it is the larger species, such as giraffe *(Giraffa camelopardalis)* and white rhino (*Ceratotherium simum*), that WB-tourists are most interested in, rather than the smaller, more common species, such as impala (*Aepyceros melampus*) and nyala (*Tragelaphus angasii*) (Maciejewski & Kerley 2014). Other studies have shown that species are more successful at attracting WB-tourists to specific sites if they are: predictable in activity or location, approachable, readily viewable i.e. they occur in open habitats, are perceived as being intelligent and/or similar in appearance and behaviour to humans (Lindsey *et al*. 2007; Jones 2009; Lorimer 2007); if they possess elements of rarity or local super abundance and/or have diurnal activity patterns (Reynolds & Braithwaite 2001). Cultural associations may also be important in shaping WB-tourist preferences for specific species (Woods 2012). It has been suggested that, for example, WB-tourists are attracted to bears, eagles, wolves, turtles and whales, as they are used as symbols in various cultures for concepts such as freedom, strength and intelligence (Woods 2012).

Wildlife viewing preferences can be diverse, with marked variation in the preferences of different types of WB-tourists (Duffus & Dearden 1990; Lindsey *et al.* 2007). In Africa (Lindsey *et al.* 2007) and Australia (Fredline & Faulkner 2001), for example, overseas and inexperienced visitors are primarily interested in large predators and mega-herbivores, whilst more experienced or return WB-tourists often seek a broader range of species to watch, are more interested in bird and plant diversity, as well as rarer, less easily observed or less high-profile mammal species (Duffus & Dearden 1990; McFarlane 1994; Martin 1997; Cole & Scott 1999).

Although wildlife viewing preferences can be diverse, it is now broadly accepted that large, charismatic vertebrate species (hereafter referred to as charismatic megafauna) are a major component of any wildlife assemblage, responsible for attracting WB-tourists of all nationalities, budgets and experiences, to specific sites around the world (Goodwin & Leader-Williams 2000; Walpole & Leader-Williams 2002; Maciejewski & Kerley 2014; Krüger 2005; Lindsey *et al.* 2007).

Charismatic megafauna are often used as flagship species to help anchor conservation campaigns, as they arouse public interest and empathy (Clucas *et al.* 2008). The use of flagship species is purely strategic, to raise awareness and financial support for conservation (Walpole & Leader-Williams 2002). However, there is concern that flagship species distort management priorities to the detriment of wider biodiversity conservation (Kerley *et al.* 2003; Andelman & Fagan 2000; Lindsey *et al.* 2007; Okello *et al*. 2008), diverting conservation action to a few glamorous species, without delivering broader biodiversity benefits (Andelman & Fagan 2000; Entwistle & Dunstone 2000; Linnell *et al.* 2000; Kerley *et al*. 2003). The success of a flagship species is determined by whether (or not) the awareness and funds they raise, and conservation action they generate, contribute to wider conservation goals rather than preservation of the flagship species alone (Dietz *et al.* 1994; Walpole & Leader-Williams 2002). This may be as simple as providing revenues for wider biodiversity conservation in the PA where the flagship species occurs or, alternatively, revenues may be redistributed to other sites (Walpole & Leader-Williams 2002).

Charismatic megafauna are also used by WBT companies in marketing campaigns, to help raise the profile of WBT destinations (Walpole & Leader-Williams 2002; Kerley *et al*. 2003). So appealing are some charismatic megafauna to WB-tourists that WBT operations at some sites are successful, even when other factors predict failure (Krüger 2005). An example of this type is western gorilla (*Gorilla gorilla*) tourism in

Rwanda, which operates with sufficient tourist numbers despite political instability in the wider region (Groom *et al.* 1991). However, there is concern that preferences of WB-tourists for charismatic megafauna may be a serious limitation to the role of WBT in conservation (Walpole & Leader-Williams 2002; Kerley *et al.* 2003; Krüger 2005; Lindsey *et al.* 2007).

When charismatic megafauna are not present in a region the market for WBT may be severely limited, even though the ecosystem might be very important in biodiversity terms (Andelman & Fagan 2000; Entwistle & Dunstone 2000; Krüger 2005). Furthermore, charismatic megafauna can be expensive to conserve because they cause damage to human livelihoods and infrastructure (Mishra 1997), or, because they are targets for poaching and require expensive anti-poaching operations (Lindsey *et al.* 2007), which can limit funds available for wider biodiversity conservation (Kerley *et al*. 2003; Maciejewski & Kerley 2014). One study found that, in Nepal, the average annual household income halved in the 1990s as a result of livestock losses to large vertebrate species (Mishra 1997). However, this study was based on self-reporting, so may have exaggerated the extent of losses. Meanwhile, in southern regions of Africa signficant numbers of domestic livestock have been lost to foot and mouth disease, transmitted by African buffallo (*Syncerus caffer*) (Bruckner *et al.* 2002; Small *et al.* 2011). Local benefits received through WBT may help offset the costs of living with charismatic megafauna (Walpole & Leader-Williams 2002). However, large assemblages of these species often exist in developing countries where governance is poor, resources required to manage species effectively are limited and corruption wastes funds intended for local communities and conservation (Eklund *et al.* 2011).

2.1.2 Measuring Wildlife Viewing Preferences

Wildlife viewing preferences are most commonly derived from site-specific surveys or interviews, using contingent valuation methods (CVMs) or structured questionnaires (Barnes *et al*. 1999; Martin-Lopez *et al*. 2007; Wood *et al*. 2013). Contingent valuation methods are a survey-based economic technique, for the valuation of a non-market resource, that assumes individual preferences can be drawn by creating a hypothetical market (Engeman *et al.* 2002). Contingent valuation methods can be used to asses an individuals' 'willingness-to-pay' for hypothetical changes in an environmental quality, for example, for the conservation of a species at a specific WBT destination (Reynisdottir *et al.* 2008; Armbrecht 2014). Measuring willingness-to-pay requires statements from individuals, usually generated through face-to-face interviews or mail/telephone surveys. Individuals are asked directly for the monetary value they would attach to the environmental good or project in question, or if they would be willing to pay a set value for a specific hypothetical outcome (Engeman *et al.* 2002). According to this method, the more an individual is willing to pay, the more valuable the resource is to them. Despite their widespread use, contingent valuation methods are heavily criticised as they are based on hypothetical, rather than actual, behaviour and often show little consideration for personal budget constraints (Reynisdottir *et al*. 2008; Wood *et al*. 2013; Armbrecht 2014). Individuals with relatively high disposable incomes can afford to pay a greater amount than people with lower disposable incomes, regardless of how highly they value the resource. Furthermore, some individuals object to putting a value on nature and therefore oppose the use of contingent valuation methods on ethical grounds. Meanwhile, structured questionnaires are often criticised because participants stated and observed preferences can differ considerably (Maciejewski & Kerley 2014), they can be expensive to carry out, and provide limited spatial and temporal coverage (Wood *et al*. 2013).

In this study, I adopt an alternative method for deriving wildlife viewing preferences. I extract data on species mentioned within a range of WBT guidebooks, travel brochures and online resources, all of which are global in scope. I assume that species mentioned by these sources help raise the profile of a site and act as a draw for WB-tourists. I use the frequency with which a species is mentioned by these sources as an index-of-attractiveness (IOA) for the species and build a modelling framework to predict IOA, based on species traits and characteristics. I focus on terrestrial mammal (TM) species, which excludes cetacean, pinnipedia and sirenia, as TM species are now recognised as a major component of any wildlife assemblage, responsible for attracting WB-tourists to specific destinations (Lindsey *et al*. 2007; Clucas *et al*. 2008; Smith *et al*. 2012; Maciejewski & Kerley 2014; Arponen *et al*. 2014).

2.2 METHODS

2.2.1 Data Collection

Using the PanTHERIA (2009) and Wilson and Reeder (2005) databases, I built a comprehensive list of the 5286 TM species of the world. I used synonym information from the International Union for the Conservation of Nature (IUCN) Red List database to match up the scientific names from the two sources (IUCN 2016). I concentrated on a subset of 4178 TM species, which excludes chiroptera (bats), as they are small, nocturnal species, with limited trait data available, and are rarely used to attract WB-tourists to specific sites. It also excludes humans (*Homo sapiens),* domesticated cat (*Felis catus)* and domesticated guinea pig (*Cavia porcellus)*, as humans and domestic animals are not considered as wildlife species. I compiled body mass, diet, time partitioning, IUCN Red List status, taxonomic order and range size data from various sources, for all 4178 TM species of interest (Table 2.1). IUCN Red List status, taxonomic order and range size data were available for all 4178 TM species. However, diet type, time partitioning and body mass data were only available for 2438, 2406 and 2683 TM species, respectively, resulting in complete trait datasets for 2370 TM species (Table 2.2).

Diet types were: (1) herbivore (feeds on plants, not vertebrate and/or invertebrate species), (2) omnivore (feeds on vertebrate and/or invertebrate species, includes any other categories), or (3) carnivore (feeds on vertebrate and/or invertebrate species only). Time partitioning strategies were: (1) nocturnal or (2) diurnal (includes crepuscular and cathemeral). IUCN Red List status categories were: critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), conservation dependent (CD), least concern (LC), or data deficient (DD). CD taxa are the focus of continuing conservation programmes, the cessation of which would

result in the taxon qualifying for one of the three threatened categories: CR, EN or VU (IUCN 2016). NT taxa do not qualify for CD but are close to qualifying for VU, whilst LC taxa do not qualify for CD or NT (IUCN 2016). A taxon is DD when there is inadequate information to make an assessment of its risk of extinction (IUCN 2016).

Range size was estimated using spatial distribution maps, downloaded from the IUCN online database (Table 2.1). Range data were transferred onto an equal area grid, in Behrman projection, with a cell size of 1° latitude by 1° longitude at 30°N and 30°S latitude (Orme *et al*. 2005; Fritz & Rahbek 2012; Huang *et al.* 2012). An equal area grid enables spatially unbiased comparisons among grid cells. A species was considered to occur in a cell if the species' range polygon and grid cell overlap was greater than, or equal to, 10%; a conservative threshold chosen to ensure the representation of small range species in the analysis. Range size was defined by the number of equal area grid cells that intersected the range polygon of a TM species.

I compiled a database of all the TM species mentioned by all available WBT guidebooks, travel brochures and online resources with comprehensive global coverage, published within the past 20 years, along with details of the sites with which the TM species were associated (Table 2.3). Each time that a species was mentioned in one of the sources it was recorded, along with details of the site. WBT brochures frequently advertised multiple tours with overlapping itineraries. Consequently, specific sites where often mentioned in association with the same TM species multiple times within a single source. To overcome the issue of overrepresentation, site-species duplicates within any single source were excluded from the analyses. This resulted in a list of 8612 unique site-species combinations of 773 different TM species and 536 different sites. The total number of unique site-species combinations that included a specific TM species (i.e. the total number of times a TM species was

mentioned by the sources, in association with a unique site), was used as the TM species' index-of-attractiveness (TM-IOA).

All sources were targeted at relatively inexperienced WB-tourists, with broad wildlife viewing interests, and provide readers with advice on which wildlife species to see, where and when. WBT books often focus on sites targeted by the mass WBT market, whilst online resources can include details for less developed sites. Using a diversity of sources ensured data were collected across a wide range of protected areas, rather than focusing on just the most attractive protected areas with the highest visitation rates. However, the sources were heavily biased towards the Anglosphere, specifically the preferences, language and income groups most represented by the readers. Care should, therefore, be taken when applying the results from this study across the wider WBT community. Future studies should derive TM-IOA values from a broader range of sources, to help reduce this bias.

2.2.2 Data Analysis

Varying degrees of taxonomic specificity were used, at times, by most sources when advertising the presence of different TM species at WBT destinations. Occasional references were made to higher orders of classification, for example 'antelope' or 'monkeys'. These data were recorded in the database but were excluded from subsequent analyses: only references made to individual species were included. Sub-species, such as the kermode bear (*Ursus americanus kermodei)* and dingo (*Canis lupus dingo)*, were analysed under their species names i.e. brown bear (*Ursus americanus)* and wolf (*Canis lupus)*. This was necessary in order to increase the consistency and compatibility of the database derived from this study with the IUCN and PanTHERIA databases used in subsequently analyses. However, treating

subspecies at the species level may have reduced the accuracy of the model's predictions as, for example, a tourist wanting to see a dingo is not the same as a tourist wanting to see a wolf.

Table 2.1: List of species traits used to explain variation in the attractiveness of terrestrial mammal species, and the sources from which the trait data were derived.

Trait	Source
Body Mass	PanTHERIA (available at: http://esapubs.org/Archive/ecol/E090/184/default.htm) CRC Handbook of Mammalian Body Mass (Silva & Downing 1995)
Diet Type	PanTHERIA (available at: http://esapubs.org/Archive/ecol/E090/184/default.htm) Animal Diversity Web (available at: http://animaldiversity.org/)
IUCN Red List Status	IUCN Red List of Threatened Species Database (available at: http://www.iucnredlist.org/) **Mammal Species of the World, 3rd edition** (Wilson & Reeder 2005)
Range Size	IUCN Red List of Threatened Species Database (available at: http://www.iucnredlist.org/)
Taxonomic Order	PanTHERIA (available at: http://esapubs.org/Archive/ecol/E090/184/default.htm) **Mammal Species of the World, 3rd edition** (Wilson & Reeder 2005)
Time Partitioning Strategy	Bennie *et al*. (2014) Animal Diversity Web (available at: http://animaldiversity.org/)

Table 2.2: Number of terrestrial mammal species (TM) in each taxonomic order, with trait data available.

Taxonomic Order	Number of TM species	Number of TM species with trait data available					Number of TM species with all trait data available
		IUCN Red List Status	Range Size	Diet Type	Time Partitioning	Body Mass	
Afrosoricida	51	51	51	39	39	39	39
Artiodactyla	240	240	240	201	201	201	201
Carnivora	255	255	255	212	212	212	212
Cingulata	21	21	21	20	20	20	20
Dasyuromorphia	71	71	71	46	60	60	46
Dermoptera	2	2	2	2	2	2	2
Didelphimorphia	87	87	87	64	64	64	64
Diprotodontia	143	143	143	92	114	114	92
Erinaceomorpha	24	24	24	19	12	12	12
Hyracoidea	4	4	4	4	4	4	4
Lagomorpha	92	92	92	60	60	60	60
Macroscelidea	15	15	15	14	14	14	14
Microbiotheria	1	1	1	1	1	1	1
Monotremata	5	5	5	3	3	3	3
Notoryctemorphia	2	2	2	1	1	1	1
Paucituberculata	6	6	6	6	6	6	6
Peramelemorphia	21	21	21	15	15	15	15
Perissodactyla	17	17	17	14	12	12	12
Pholidota	8	8	8	7	7	7	7
Pilosa	10	10	10	9	9	9	9
Primates	375	375	375	264	264	264	264
Proboscidea	3	3	3	3	3	3	3
Rodentia	2276	2276	2276	1140	1081	1358	1081
Scandentia	20	20	20	17	17	17	17
Soricomorpha	428	428	428	184	184	184	184
Tubulidentata	1	1	1	1	1	1	1
Total	**4178**	**4178**	**4178**	**2438**	**2406**	**2683**	**2370**

Table 2.3: List of wildlife-based tourism guidebooks, travel brochures and online resources, with comprehensive global coverage. The total number of times a terrestrial mammal species was mentioned by the sources, in association with a site, was used as the species' index of attractiveness.

Source Type	Reference	Country of Publication
Books	Nature Journeys (Holing 1996)	England
	Nature's Strongholds (Riley 2005)	USA
	Parques y reservas del mundo (Santolalla 2006)	Spain
	100 Animals (Garbutt 2007)	England
	Global Safari (Parry 2007)	England
	Destination Wildlife (Brodowsky 2009)	USA
	A Year of Watching Wildlife (Lukas 2009)	USA
	Ultimate Wildlife Experiences (Carwardine 2011)	England
	Swimming with Dolphins, Tracking Gorilla (Wood 2012)	England
	Wildlife Travel (Gray 2012)	England
Brochures	Wildlife Worldwide (Scott & Scott 2015)	England
	Natural World Safaris (Bolsover 2014)	England
	Naturetrek (Tucker *et al*. 2015)	England
	Exodus (Goldstein 2015)	England
	The Travelling Naturalist (The Travelling Naturalist 2016)	England
Online Resources	Exsus (available at: www.nathab.com/our-trips/)	England
	Nathab (available at: www.exsus.com/holiday-types/wildlife-holidays)	USA
	Wildwings (available at: www.wildwings.co.uk/holidays/mammal-watching)	England

2.2.3 Statistical Analysis

Statistical analyses were conducted on the 2370 TM species, for which all trait data were available (Table 2.2). Only 773 (32.6%) of these TM species were selected at least once by the sources and were subsequently allocated a TM species index-of-attractive (TM-IOA) value greater than zero. To account for zero-inflation and over-dispersion in the TM-IOA data, two separate analyses were performed. First, a binary generalised linear model (GLM) was used to predict whether species were selected (or not) in any of the sources, hereafter referred to as a TM species' likelihood-of-selection (TM-LOS), using the 'MASS' package in R (R Development Core Team 2015). Second, a negative binomial GLM was used to predict the TM-IOA values for the 773 TM species that were selected at least once by the sources, using the 'MASS' package in R (R Development Core Team 2015). Both models included as explanatory variables: taxonomic order, time partitioning strategy, body mass, range size, IUCN Red List status and diet. Data exploration suggested that the relationship between body mass and TM-IOA varies across the three diet types. Consequently, models also included an interaction between body mass and diet.

To avoid selecting overly complex models I used model selection, applying a two-step selection criterion (following Richards 2008) to evaluate the top candidate models. I initially retained models if they had a delta Akaike Information Criterion (ΔAIC) within six units of the model of best fit (Richards 2008). Next, to remove overly complex models, I disregarded models with a higher AIC value than any simpler nested models.

To explore the effect of variation in single parameters on a TM species' (1) likelihood-of-selection (TM-LOS), and (2) index-of-attractiveness (TM-IOA), I sequentially varied individual parameters in both the binary GLM (for TM-LOS) and negative binomial

GLM (for TM-IOA), whilst holding all other parameters in the model at a fixed value. The fixed parameter dataset was centred on the mean trait values for order artiodactyla: IUCN Red List status (NT), body mass (122.1 kg), time partitioning (diurnal), diet type (herbivore) and range size (1145 terrestrial grid cells). These values and groups were used for centering as they were the average trait values for the most common order of terrestrial mammal species.

The binary GLM produced probabilistic predictions. In order to evaluate the model's ability to predict whether (or not) a TM species was mentioned by the reviewed sources, I applied an optimal threshold value to convert these into the original binary format (Guisan & Zimmermann 2000; Allouche *et al.* 2006). I used the maximum value of Cohen's kappa (k) as the threshold value, to distinguish a subset of false positive and negative predictions (McHugh 2012). Cohen's kappa was used, as opposed to a threshold of 0.5, as Cohen's kappa accounts for base rate. It was calculated using the following formula, where n = number of subjects, n_a = number of agreements and n_ε = number of agreements due to chance:

Equation 2.1: $$\kappa = \frac{n_a - n_\varepsilon}{n - n_\varepsilon}$$

I used the area under the curve (AUC) of a receiver operating characteristic (ROC) plot to evaluate the accuracy of the binary GLM (Allouche *et al.* 2006). I defined AUC values of 0.8< as a null model, 0.8<AUC<0.9 as a fair model, 0.9<AUC<0.95 as a good model, and 0.95<AUC<1.00 as a very good model (Thuiller *et al.*(2006)

Statistical analyses were performed using R version 3.2.4 (R Development Core Team 2016).

2.3 RESULTS

Model selection yielded two candidate binary GLMs (for TM-LOS) and two candidate negative binomial GLMs (for TM-IOA) (Table 2.4). The best binary GLM explained 45.7% of the observed variation in TM-LOS and was considered a good model, with an AUC of 0.92 (Table 2.4). In the best binary GLM, a significant positive correlation was found between body mass and TM-LOS, range size and TM-LOS, and IUCN Red List status and TM-LOS (Figures 2.3A, 2.3C and 2.3E), and TM species in orders didelphimorphia and rodentia were significantly less likely to be selected as WBT-attractant species (defined as TM species in Figure 2.1, quadrants A and B) than species in other taxonomic orders (Table 2.5).

The best negative binomial GLM explained 65.6% of the observed variation in TM-IOA (Table 2.4). A strong positive correlation was found between the actual and predicted TM-IOA values, by the best negative binomial GLM (Linear Regression; $F_{1,771} = 696.1$, $P < 0.01$; Adjusted $R^2 = 0.474$) i.e. the negative binomial GLM did well at predicting the number of times a TM species was selected by the sources (Figure 2.2). In the best negative binomial GLM: body mass and range size were positively related to TM-IOA (Figures 2.3B and 2.3D), and critically endangered TM species were significantly more likely to be selected as WBT-attractant species than species in other IUCN Red List status categories (Figure 2.3F; Table 2.6). Diet type, time partitioning strategy and taxonomic order had no effect on TM-IOA. However, a significant interaction was found between body mass and diet type (Table 2.7). No difference was found in the relationship between body mass and TM-IOA for carnivore, omnivore and herbivore TM-species with body masses less than 1 kg. However, once this mass is exceeded, carnivorous species show a greater increase in TM-IOA with increasing body mass compared to omnivorous and herbivorous species (Figure 2.4).

Table 2.4: Top candidate binary generalised linear models (GLMs) and negative binomial GLMs i.e. have ΔAIC values that are ≤6 (Richards 2008). Maximum log-likelihoods (LL), ΔAICs and R^2 values are shown for each model. Df is the degrees of freedom in a given model. (+) and (N/A) indicate which variables are included or excluded in each model, respectively. (*) indicates the best binary GLM and best negative binomial GLM.

Model Name	Model Number	Logged Body Mass	Logged Range Size	IUCN Red List Status	Taxonomic Order	Diet Type	Time Partitioning	Body Mass and Diet Interaction	Df	LL	ΔAIC	R^2 Value
Binary GLM	1	+	+	+	+	N/A	+	N/A	34	-875.291	0	0.449
Binary GLM	2 *	+	+	+	+	N/A	N/A	N/A	33	-877.812	2.983	0.457
Negative binomial GLM	1	+	+	+	+	N/A	N/A	+	36	-2171.743	0	0.632
Negative binomial GLM	2 *	+	+	+	N/A	N/A	N/A	+	13	-2197.344	2.074	0.656

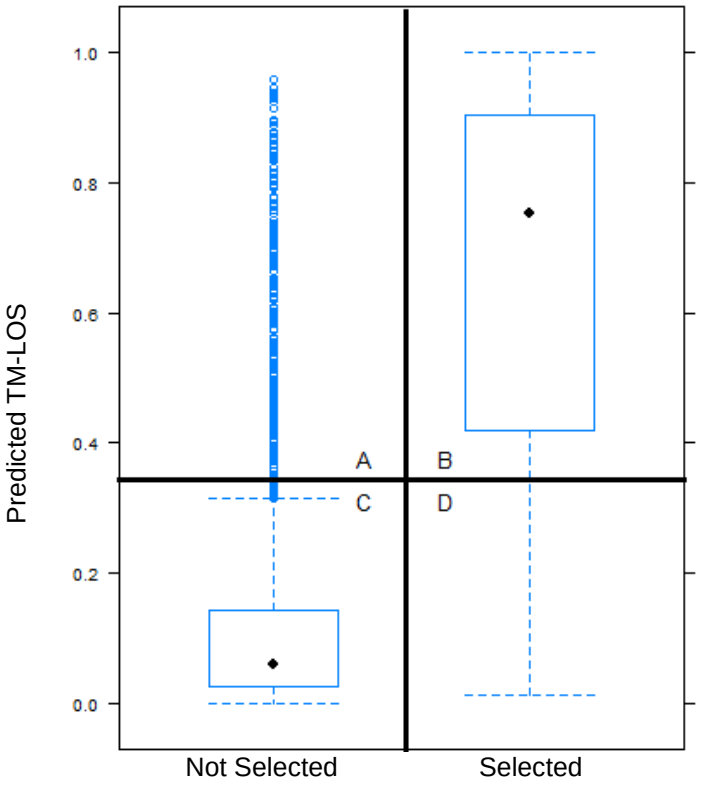


Figure 2.1: Boxplot compairson of terrestrial mammal (TM) species selected and not selected by the sources (x-axis) against their predicted likelihood of being selected as a wildlife-based tourism (WBT) attractant species, by the best binary GLM (y-axis). The maximum Cohen's kappa (0.345) was used as the threshold value, to distinguish a subset of false positive and negative predictions. (A) False positive WBT-attractant species, (B) True WBT-attractant species, (C) Unattractive TM species, (D) False negative WBT-attractant species. AUC = 0.92 predicted, (n = 2370).

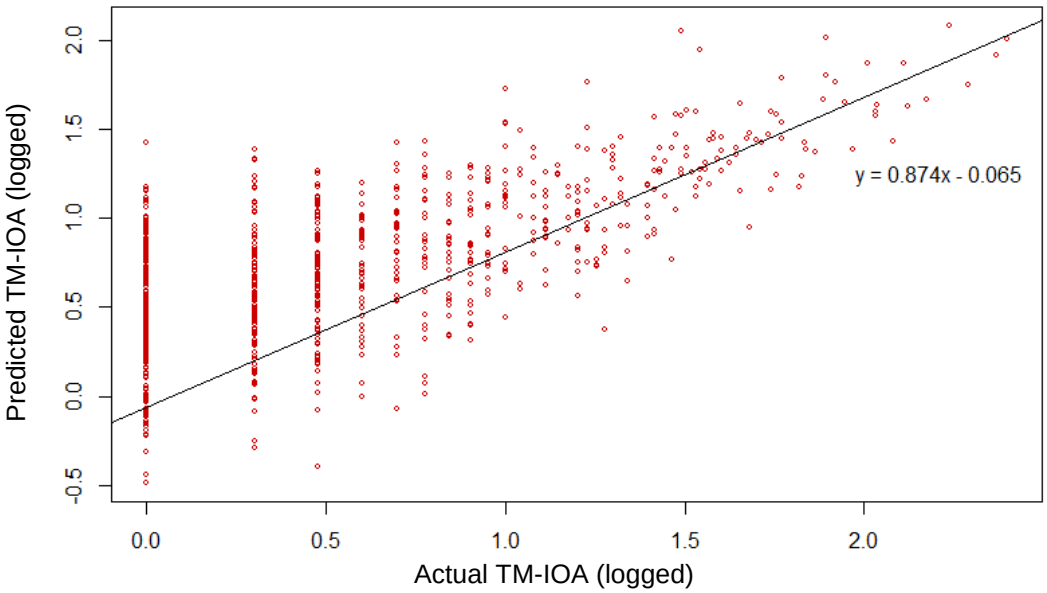


Figure 2.2: Logged actual and predicted number of times a terrestrial mammal (TM) species was selected (TM-IOA), by the sources (x-axis), and by the best negative binomial GLM (y-axis) respectively, for all TM species that were selected at least once by the sources. Significant linear regression line is shown. Adjusted R^2 = 0.474 (n = 773).

Table 2.5: Strength of effect and significance of terrestrial mammal (TM) species' traits in predicting whether (or not) a TM species will be selected as a wildlife-based tourism attractant species (defined as TM species in Figure 2.1, quadrants A and B), based on the best binary GLM's predictions. P values significant at 5% levels are shown.

	Effect Size	Standard Error	z value	P
Intercept (taxonomic *order: afrosoricida, IUCN Red List status category: DD*)	-6.02	0.83	-7.27	<0.01
Logged Body Mass	0.82	0.15	5.31	<0.01
Logged Range Size	1.01	0.09	11.50	0.01
IUCN Red List Status:				
LC	0.83	0.26	3.25	0.01
NT	1.51	0.30	5.09	0.01
VU	1.57	0.30	5.27	<0.01
EN	1.76	0.31	5.64	<0.01
CR	2.15	0.38	5.67	<0.01
Taxonomic Order:				
Didelphimorphia	-1.56	0.77	-2.04	0.04
Rodentia	-1.25	0.63	-1.98	0.05

Table 2.6: Strength of effect and significance of terrestrial mammal (TM) species' traits in predicting the number of times a TM species is mentioned by the sources, based on the best negative binomial GLM's predictions. P values significant at 5% levels are shown.

	Effect Size	Standard Error	z value	P
Intercept (taxonomic o*rder: afrosoricida, IUCN Red List status category: DD*)	-2.46	0.26	-9.39	<0.01
Logged Body Mass	0.77	0.05	15.50	<0.01
Logged Range Size	0.50	0.04	12.27	<0.01
IUCN Status:				
CR	0.47	0.18	2.60	0.01
Body Mass and Diet Interaction	0.31	0.12	2.63	0.01

A B

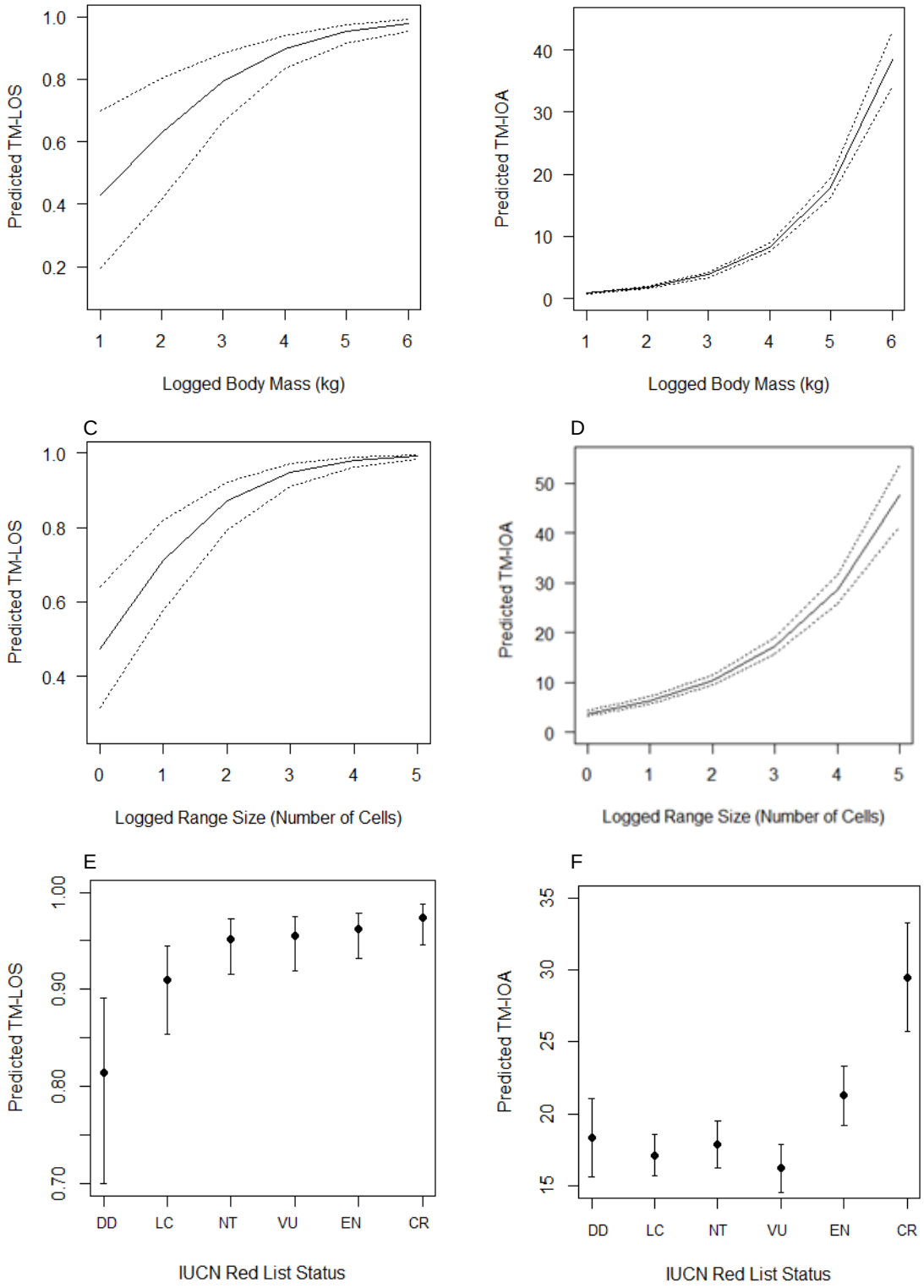


Figure 2.3: Effect of (A) logged body mass, (C) logged range size, and (E) IUCN Red List status on the predicted likelihood of being selected (TM-LOS) as a wildlife-based tourism attractant species (defined as terrestrial mammal (TM) species in Figure 2.1, quadrants A and B), based on the best binary GLM's predictions. Effect of (B) logged body mass, (D) logged range size, and (F) IUCN Red List status on the number of times a TM species will be selected (TM-IOA), based on the best negative binomial GLM's predictions. Logged range size is given in terms of the number of equal area grid cells, in Behrman projection, with a cell size of 1° latitude by 1° longitude, that a species' range polygon overlapped by more than 10%. Solid lines represent the best model predictions. Dashed lines and error bars represent ± 1 standard error (SE) of the mean.

It is interesting to compare the shape of the predicted TM-LOS and TM-IOA curves in Figure 2.3. The predicted TM-LOS curves have a convex shape (Figures 2.3A, 2.3C and 2.3E). As the trait value increases, the rate of increase in predicted TM-LOS decreases. In comparison, the predicted TM-IOA curves have a concaved shape (Figures 2.3A, 2.3C and 2.3E). As the trait value increases, the rate of increase in predicted TM-IOA increases.

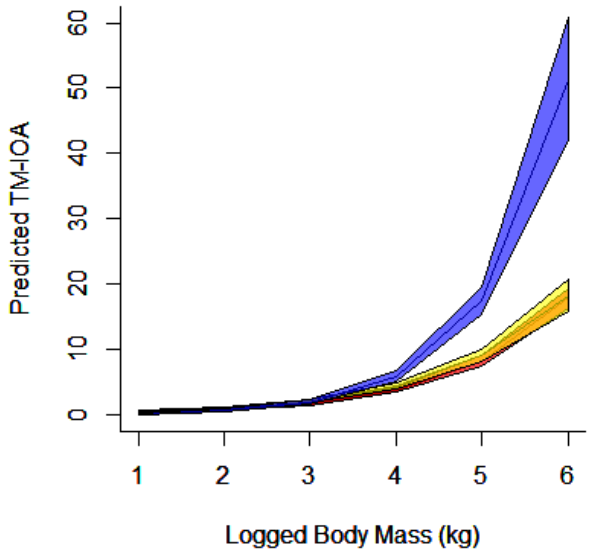


Figure 2.4: Effect of logged body mass on the predicted number of times a terrestrial mammal (TM) species is mentioned (TM-IOA) for carnviore (blue), omnivore (yellow) and herbivore (red) species. Solid line in centre of each shaded areas represents the best negative binomial GLM's predictions. Shaded areas represent ± 1 standard error (SE) of the mean.

TM species in Figure 2.1 quadrants (B) and (D) were selected at least once by the reviewed sources, whilst TM species in Figure 2.1 quadrants (A) and (C) were not selected by the sources. TM species in Figure 2.1 quadrant (A) are hereafter referred to as 'false positive WBT-attractant species'. The number of TM species in each quadrant of Figure 2.1 is presented in Table 2.7. The majority of TM species in Figure 2.1, quadrant (A) are diurnal primate (apes and monkeys), or carnivora (wolves, bears and large felids) species. The majority of TM species in quadrant (B) are large, diurnal primate or artiodactyla (antelopes and deer) species, whilst the majority of TM species in quadrants (C) and (D) are small, nocturnal rodents (Table 2.5).

Table 2.7: Number, taxonomy, average body mass, and time partitioning strategies of terrestrial mammal (TM) species in each quadrant of Figure 2.1.

Quadrant	Number of TM species	Average body mass of TM species ± 1 standard error (kg)	Ratio of Diurnal : Nocturnal TM species	Percentage of TM species in each taxonomic order
A	248	13.93 ± 4.03	1:1	Primates (33%) Carnivora (23%) Other (44%)
B	615	77.91 ± 13.45	3:2	Artiodactyla (30%) Primates (27%) Other (43%)
C	1643	0.29 ± 0.02	3:7	Rodentia (71%) Soricomorpha (10%) Other (19%)
D	158	0.57 ± 0.07	2:3	Rodentia (48%) Diprotodontia (14%) Other (38%)

Table 2.8 lists TM species with the (1) highest actual TM-IOA values, based on data extracted from the sources, (2) highest predicted TM-IOA values, derived from the best negative binomial GLM, (3) most negative residual values, and (4) most positive residual values. Residual values were calculated by subtracting the predicted TM-IOA values from the actual TM-IOA values for each species, such that: TM species with negative residuals received lower predicted than actual TM-IOA values (were under-represented by the best negative binomial GLM), whilst TM species with positive residuals received higher predicted than actual TM-IOA values (were over-represented by the best negative binomial GLM). Table 2.9 lists TM species with the highest and lowest relative residual values, based on the negative binomial GLM's predictions. Relative residual values were calculated by dividing residual values by predicted values.

Table 2.8: Terrestrial mammal (TM) species with the highest actual and predicted index-of-attractiveness (TM-IOA) values, and highest and lowest residual values. TM-IOA is defined as the number of times a TM species is selected by the sources. Predictions are based on the best binomial GLM's predictions. Residual values were calculated by subtracting the predicted TM-IOA values from the actual TM-IOA values, for each species.

Rank	TM species with highest actual TM-IOA	Actual TM-IOA	TM species with highest predicted TM-IOA	Predicted TM-IOA	TM species with lowest residual values	Residual	TM species with highest residual values	Residual
1	Leopard (*Panthera pardus*)	251	Lion (*Panthera leo*)	141.86	Leopard (*Panthera pardus*)	-128.34	African Forest Elephant (*Loxodonta cyclotis*)	94.17
2	African Bush Elephant (*Loxodonta africana*)	234	African Forest Elephant (*Loxodonta cyclotis*)	129.17	Wolf (*Canis lupus*)	-126.31	White Rhinoceros (*Ceratotherium simum*)	62.29
3	Wolf (*Canis lupus*)	195	Leopard (*Panthera pardus*)	122.66	African Bush Elephant (*Loxodonta africana*)	-113.67	Cougar (*Puma concolor*)	27.59
4	Lion (*Panthera leo*)	172	African Bush Elephant (*Loxodonta africana*)	120.33	Brown Bear (*Ursus arctos*)	-106.20	Kouprey (*Bos sauveli*)	26.94
5	Brown Bear (*Ursus arctos*)	149	Asian Elephant (*Elephas maximus*)	105.78	Wild Boar (*Sus scrofa*)	-95.13	Asian Elephant (*Elephas maximus*)	22.78
6	African Buffalo (*Syncerus caffer*)	132	Cougar (*Puma concolor*)	105.59	African Buffalo (*Syncerus caffer*)	-81.86	Argali (*Ovis ammon*)	22.36
7	Tiger (*Panthera tigris*)	129	White Rhinoceros (*Ceratotherium simum*)	93.29	Common Hippopotamus (*Hippopotamus amphibious*)	-74.44	Marsh Deer (*Blastocerus dichotomus*)	21.98
8	Wild Boar (*Sus scrofa*)	120	Tiger (*Panthera tigris*)	82.05	Giraffe (*Giraffa Camelopardalis*)	-73.00	Derby Eland (*Taurotragus derbianus*)	21.49
9	Red Deer (*Cervus elaphus*)	109	Spotted Hyena (*Crocuta crocuta*)	73.80	Red Deer (*Cervus elaphus*)	-69.27	Lichtenstein's Hartebeest (*Alcelaphus lichtensteinii*)	20.91
10	Giraffe (*Giraffa Camelopardalis*)	108	Cheetah (*Acinonyx jubatus*)	73.56	American Black Bear (*Ursus americanus*)	-64.05	Hairy-nosed Wombat (*Lasiorhinus krefftii*)	20.34

Table 2.9: Terrestrial mammal (TM) species with the highest and lowest relative residual values. Relative residuals were calculated by dividing residual values by predicted index-of-attractiveness (TM-IOA) values. Predicted TM-IOA values are defined as the predicted number of times a TM species is mentioned by the sources, by the best negative binomial GLM. Actual TM-IOA values (based on data extracted from the sources) are also given.

Rank	TM species with lowest residual/predicted values	Actual TM-IOA	Relative Residual	TM species with highest residual/predicted values	Actual TM-IOA	Relative Residual
1	Central American Squirrel Monkey (*Saimiri oerstedii*)	19	-7.08	Derby Eland (*Taurotragus derbianus*)	1	0.96
2	Berthe's Mouse Lemur (*Microcebus berthae*)	3	-6.47	Okapi (*Okapia johnstoni*)	1	0.93
3	Rufous Hare-wallaby (*Lagorchestes hirsutus*)	5	-4.94	Snow Sheep (*Ovis nivicola*)	1	0.93
4	Gray Mouse Lemur (*Microcebus murinus*)	6	-4.87	Mountain Anoa (*Bubalus quarlesi*)	1	0.92
5	Red Muntjac (*Muntiacus muntjak*)	48	-4.45	Dama Gazelle (*Nanger dama*)	1	0.92
6	European Snow Vole (*Chionomys nivalis*)	6	-4.09	Sunda Pangolin (*Manis javanica*)	1	0.92
7	Guatemalan Black Howler (*Alouatta pigra*)	22	-3.99	Kiang (*Equus kiang*)	2	0.92
8	Ermine (*Mustela ermine*)	29	-3.95	South American Brown Brocket (*Mazama gouazoubira*)	1	0.92
9	Musky Rat-kangaroo (*Hypsiprymnodon moschatus*)	6	-3.70	Cape Porcupine (*Hystrix africaeaustralis*)	1	0.91
10	Wild Boar (*Sus scrofa*)	120	-3.46	Northern Tamandua (*Tamandua mexicana*)	1	0.90

For each terrestrial grid cell of the world, the number of WBT-attractant species, defined as TM species in Figure 2.1 quadrants (A) and (B), present in any given cell was summed together to provide an estimate of the TM species assemblage attractiveness of that cell (Figure 2.7). An alternative measure of assemblage attractiveness was derived by summing the predicted TM-LOS values (from the best binary GLM) of all the TM species present in a cell (Figure 2.8), or by summing the predicted TM-IOA values (from the best negative binomial GLM) of all the TM species present in a cell (Figure 2.9). This alternative approach considers not just the number of attractive TM species present, but also their summed attractiveness values. Regions with the highest summed TM-IOA values are found in sub-Saharan Africa (Figure 2.9). The Canadian Rocky Mountains, Brazil and Indochina were also identified as regions of high summed TM-IOA, as were parts of the Middle-East. In contrast, the Caribbean, Argentina and Chile, the Sahara, Madagascar and Australasia were identified as regions of relatively low summed TM-IOA. Figure 2.5 is a map of global TM species richness, showing the number of TM species present in each grid cell, across the global terrestrial land mass. A significant positive linear relationship was found between the TM species richness and summed TM-IOA of each terrestrial grid cell (Linear regression; $F_{1,56620} = 140600$, $P<0.001$; $R^2 = 0.713$), which may help explain the visual similarities between Figures 2.5 to 2.9. This relationship is not surprising as areas with higher species richness have a greater number of TM-IOA values to sum together. An alternative approach would have been to look at the relationship between species richness and average TM-IOA in each grid cell, or between species richness and the TM-IOA of the most attractive species present in each grid cell. Figures 2.10 and 2.11 highlight regions with high summed TM-LOS and summed TM-IOA, respectively, based on the 248 false positive WBT-attractant species (defined as TM species in Figure 2.1, quadrant A). False positive WBT-attractant species are defined as TM species that were not mentioned in the WBT guidebooks, travel brochures and online resources, however,

were selected by the best binary GLM as WBT-attractant species. Highlighted regions include: the Congo Basin (Cameroon, Gabon, Republic of Congo, the Democratic Republic of Congo and Central African Republic), Indochina (Southern China, Myanmar, Laos, Vietnam, Thailand, Malaysia and Northern Indonesia) and remote, or inaccessible, regions of the Amazon (North West Brazil, around the Amazon River) (Figures 2.10 & 2.11).

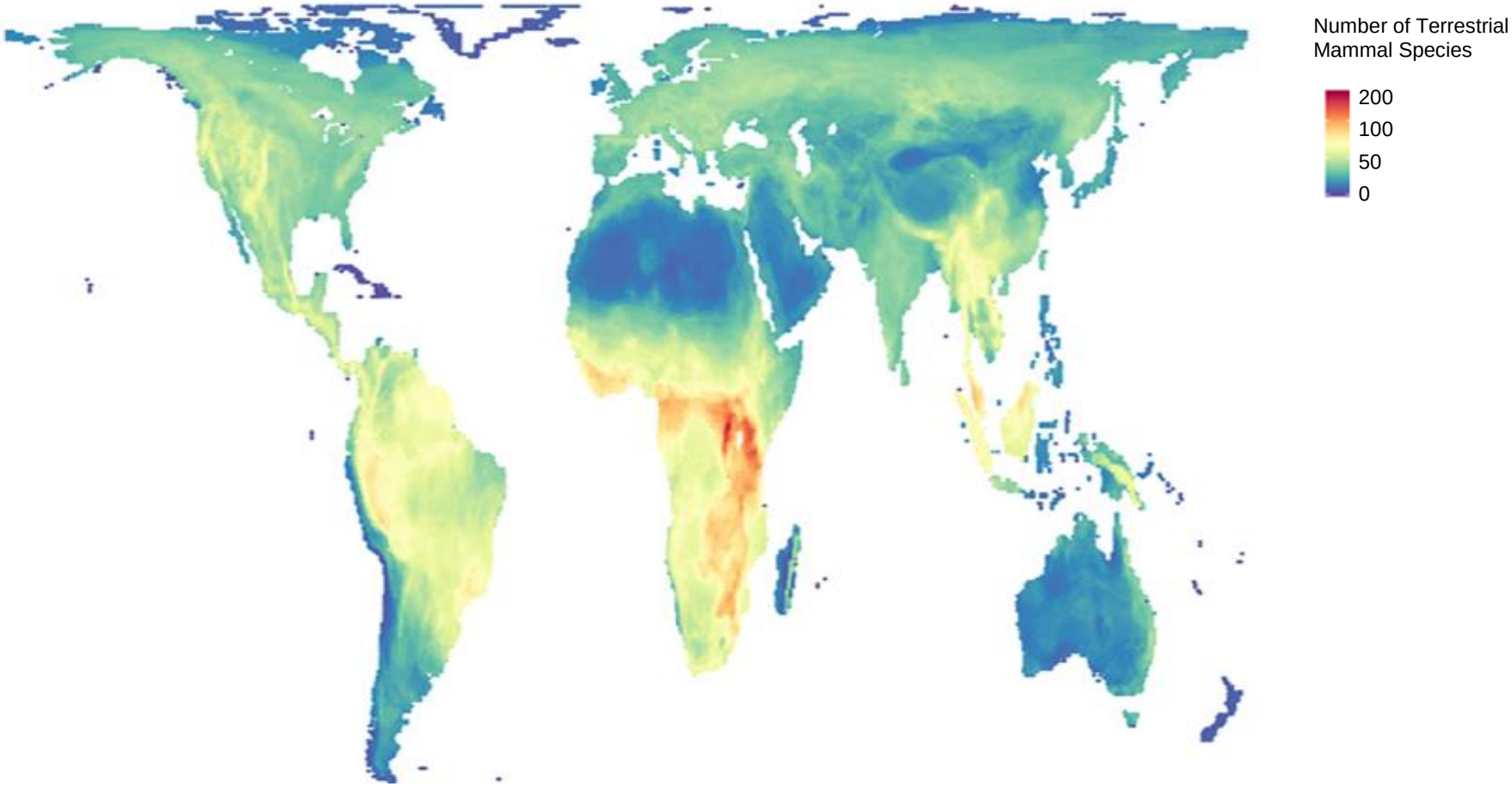


Figure 2.5: Number of terrestrial mammal species, for which all trait data were available, that are present in each terrestrial grid cell of the world (n=2370).

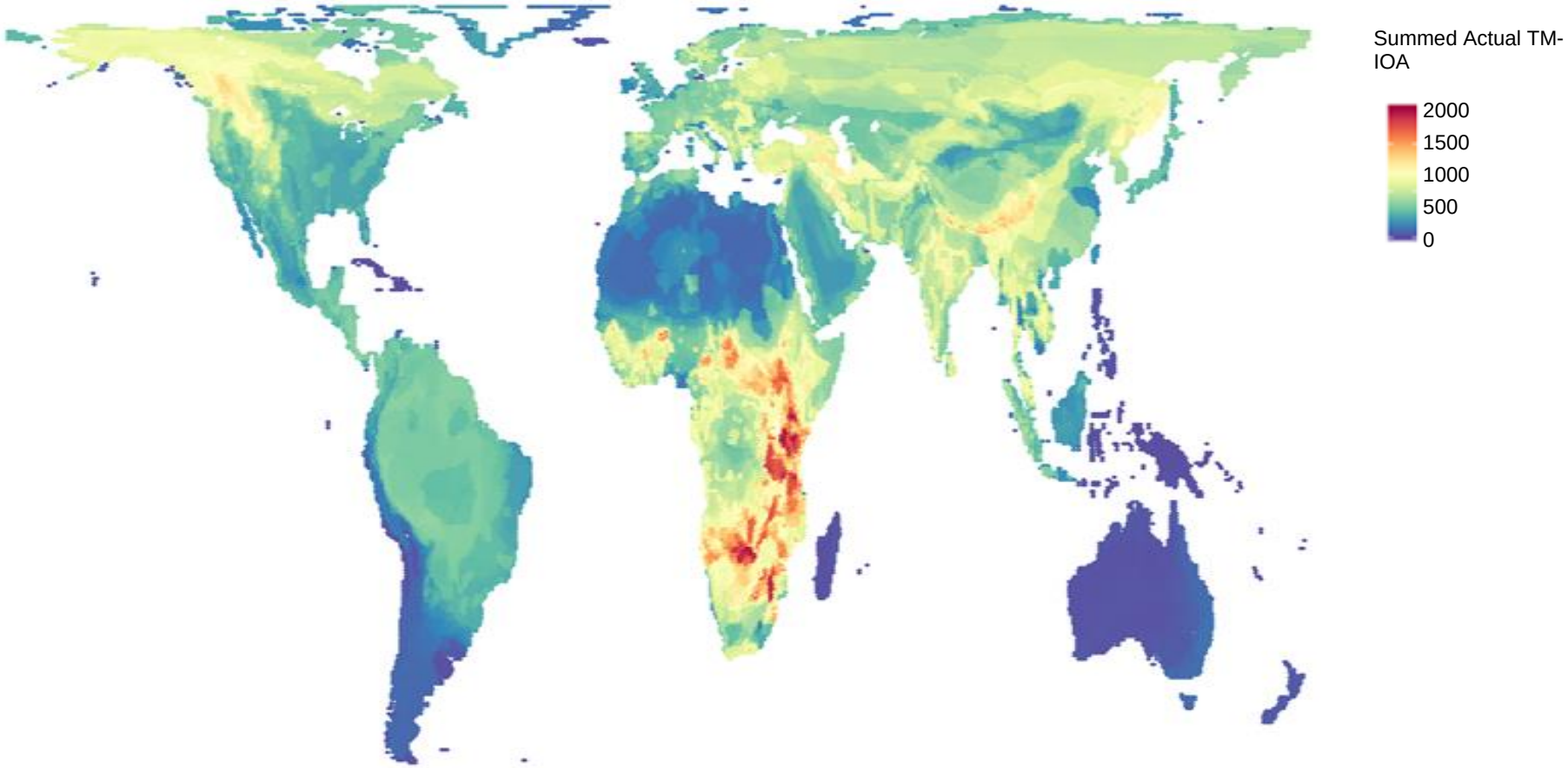


Figure 2.6: Global terrestrial mammal (TM) species assemblage attractiveness scores, based on actual index-of-attractiveness (IOA) values, derived by summing together the IOA values of all the TM species (for which all trait data were available) present in a single terrestrial grid cell. Actual IOA is defined as the number of times a TM species was mentioned by the reviewed sources (n=2370).

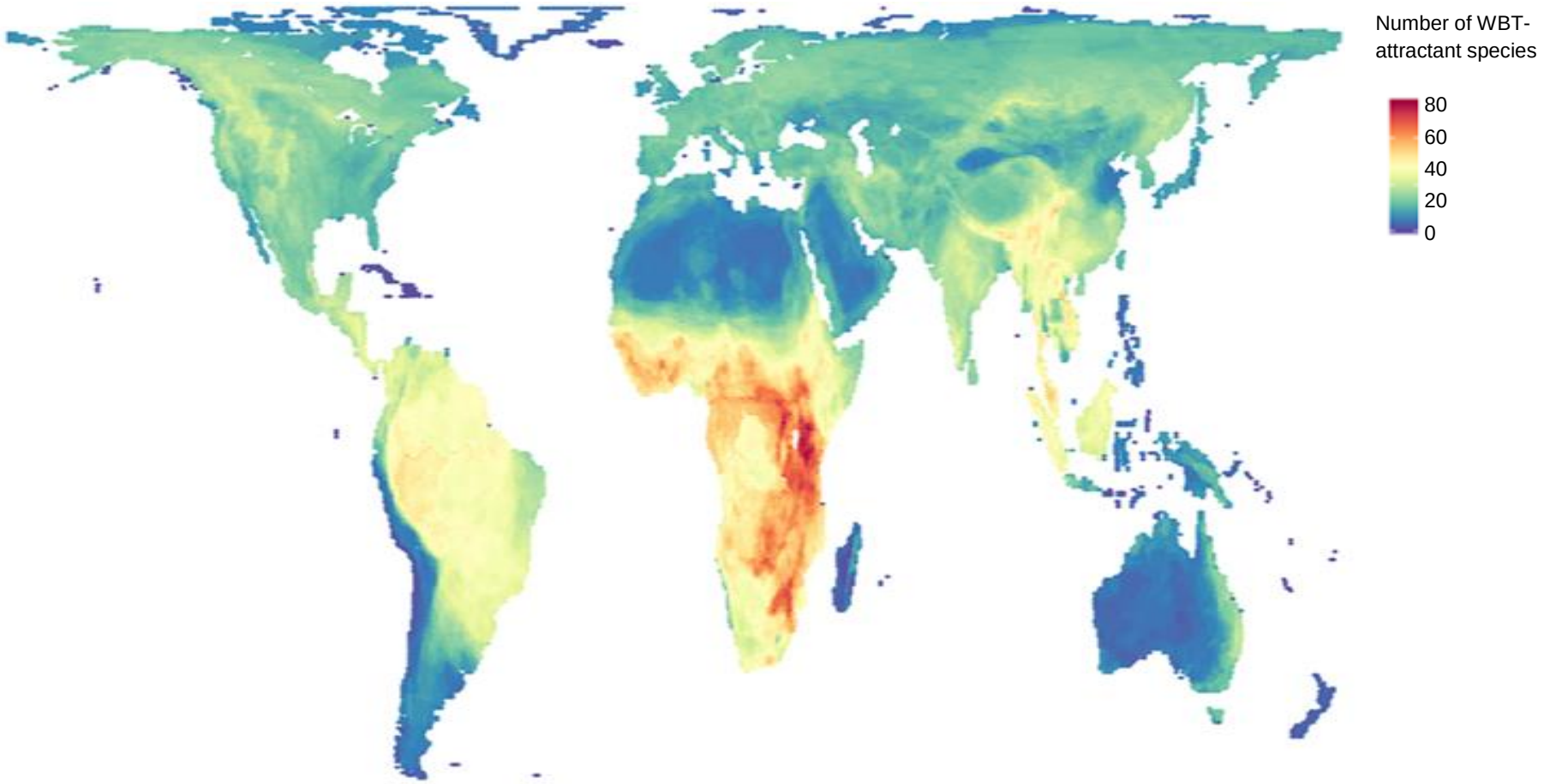


Figure 2.7: Number of wildlife-based tourism attractant species (defined as terrestrial mammal species in Figure 2.1, quadrants A and B), present in each terrestrial grid cell of the world (n=863).

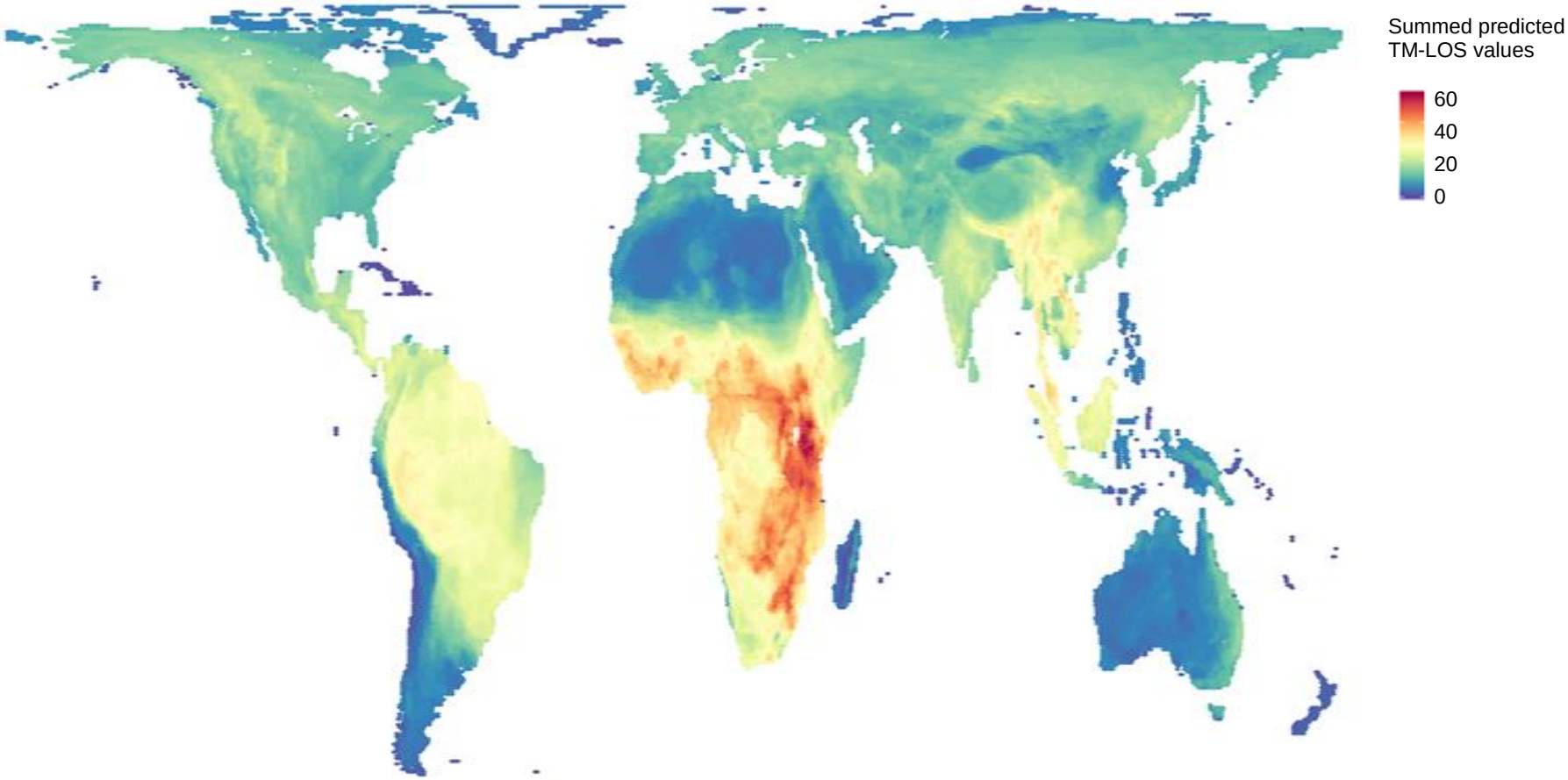


Figure 2.8: Global terrestrial mammal (TM) species assemblage attractiveness scores, based on predicted likelihood-of-selection (LOS) values, derived by summing together the predicted LOS values of all the TM species (for which all trait data were available) present in a single terrestrial grid cell. Predicted LOS is defined as the predicted likelihood of being selected as a wildlife-based tourism attractant species by the best binary GLM (n=2370).

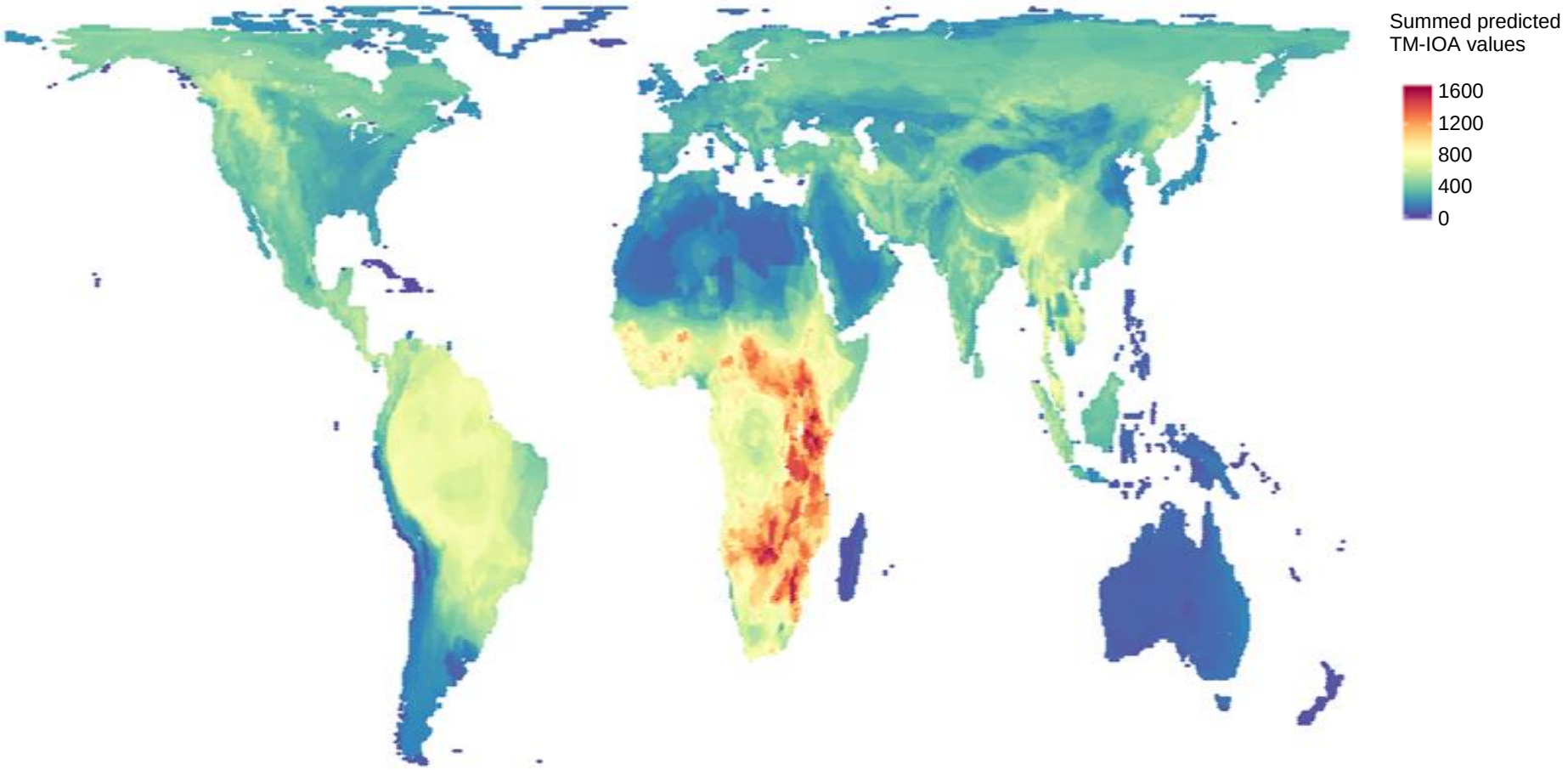


Figure 2.9: Global terrestrial mammal (TM) species assemblage attractiveness scores, based on predicted index-of-attractiveness (IOA) values, derived by summing together the predicted IOA values of all the TM species (for which all trait data were available) present in a single terrestrial grid cell. Predicted IOA is defined as the predicted number of times a TM species was mentioned by the best negative binomial GLM (n=2370).

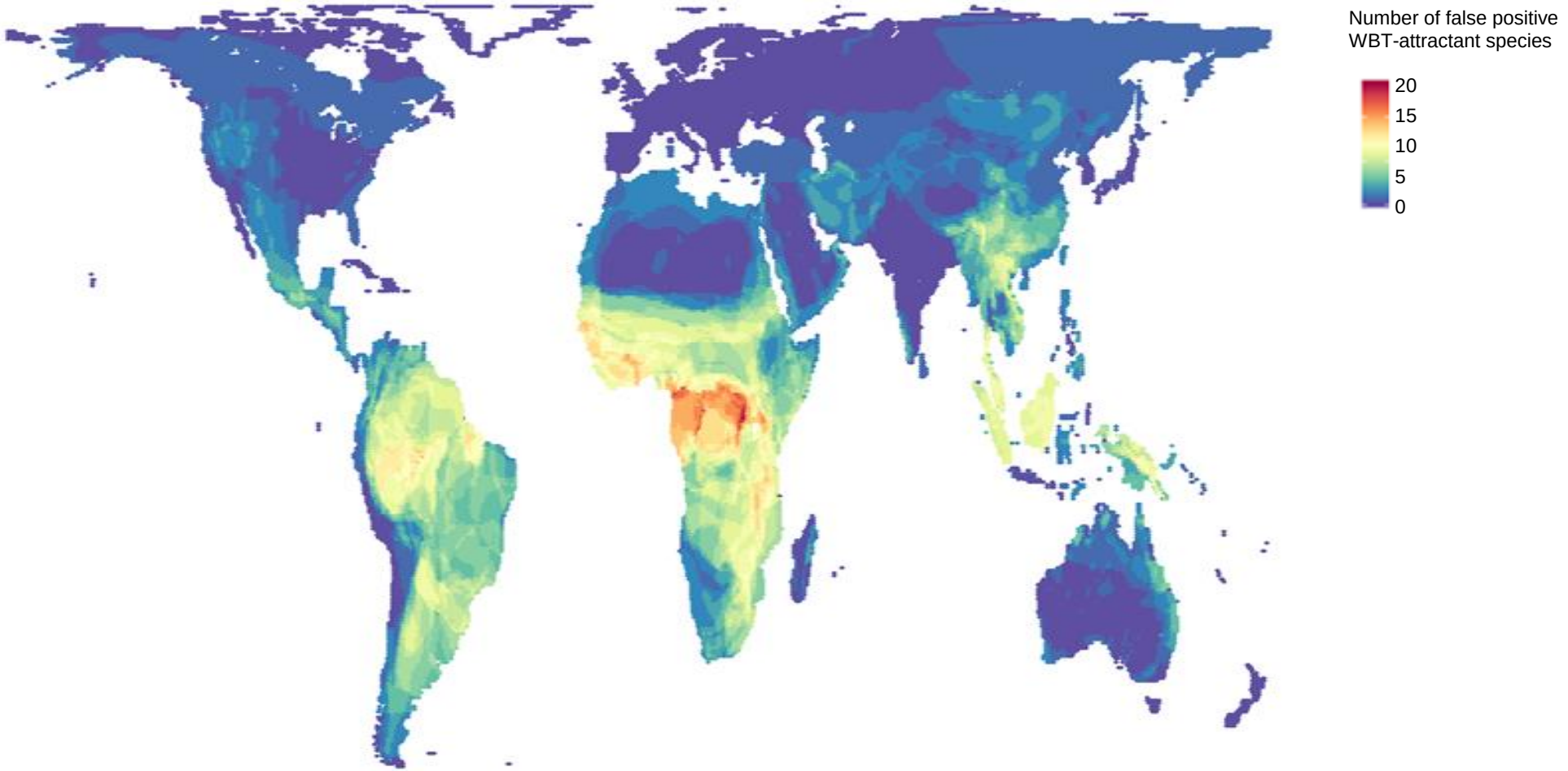


Figure 2.10: Number of false positive wildlife-based tourism (WBT) attractant species (defined as terrestrial mammal species in Figure 2.1, quadrant A), present in each terrestrial grid cell of the world (n=248).

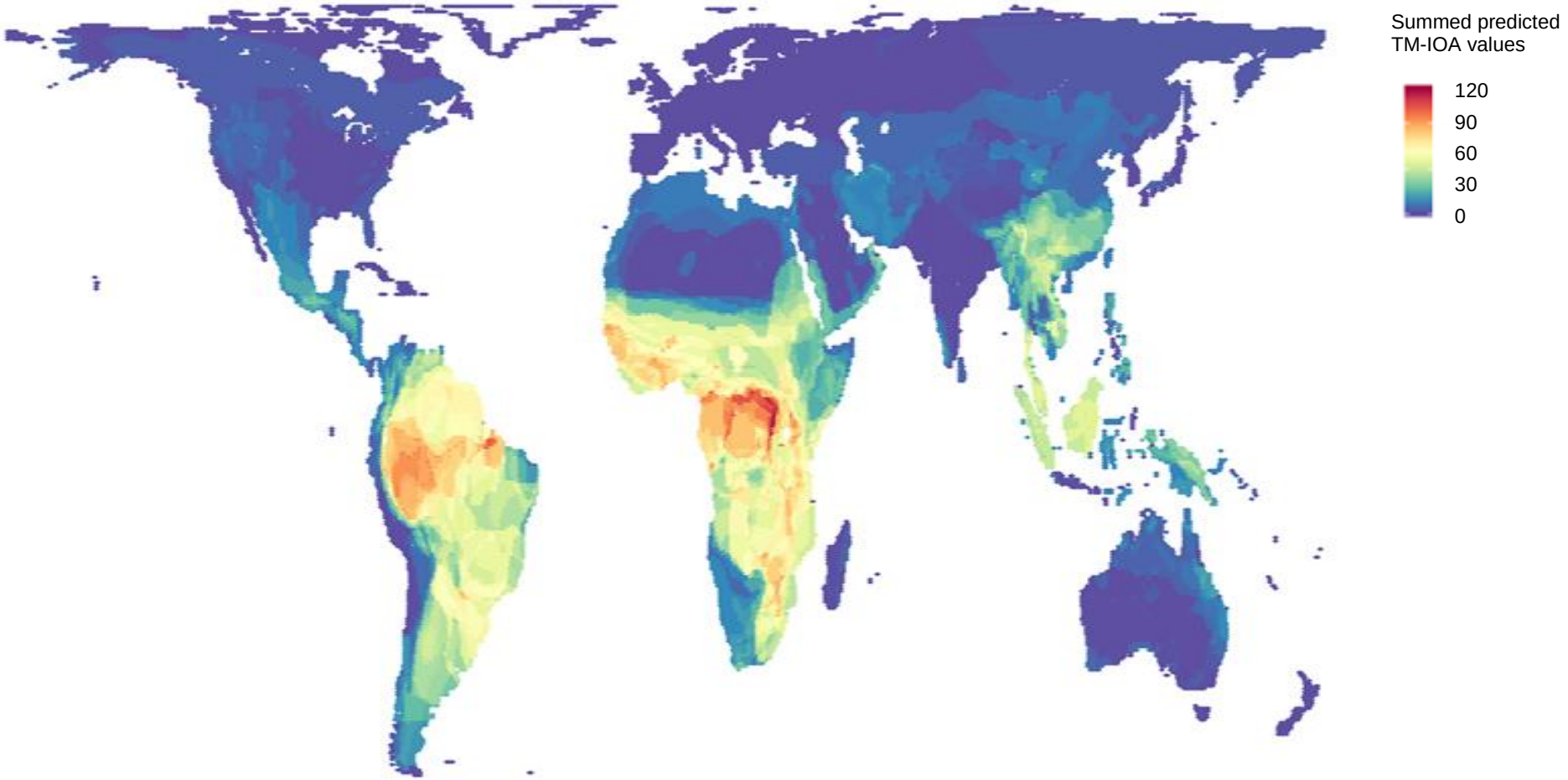


Figure 2.11: Global terrestrial mammal (TM) species assemblage attractiveness scores, based on predicted index-of-attractiveness (IOA) values, derived by summing together the predicted IOA values of all the false positive wildlife-based tourism attractant species (defined as terrestrial mammal species in Figure 2.1, quadrant A) present in a single terrestrial grid cell. Predicted IOA is defined as the predicted number of times a TM species was mentioned by the best negative binomial GLM (n=248).

2.4 DISCUSSION

2.4.1 Body Mass and Rarity

The results from this study confirm the importance of body mass and rarity (in terms of IUCN Red List status) as key traits, responsible for making TM species attractive to WB-tourists (Lindsey *et al*. 2007; Clucas *et al*. 2008; Smith *et al*. 2012; Maciejewski & Kerley 2014; Arponen *et al*. 2014). Both models predict that large, threatened TM species, such as the vulnerable lion (*Panthera leo*), vulnerable leopard (*Panthera pardus*) and near threatened white rhino (*Ceratotherium simum*), are more attractive to WB-tourists than smaller, less threatened species, such as the agile kangaroo rat (*Dipodomys agilis)* (Table 2.8). This is in accordance with previous studies that suggest large, threatened species are more valuable to WBT than smaller, more common species (Verissimo *et al*. 2011; Arponen *et al*. 2014).

WB-tourist preferences for large, threatened TM species could help motivate and incentivise tour operators and host communities who benefit financially from WBT to conserve these species and/or the habitats in which they reside (Buckley 2000; van Oosterzee 2000; Sekercioglu 2002). Large TM species often have large area requirements (Newton 1979; Gittleman *et al*. 2001; Walpole & Leader-Williams 2002), and occupy regions with higher topographic and habitat complexity, that promote higher biodiversity than sites where large TM species are not present (Rosenzweig 1995; Sergio *et al.* 2006). Consequently, the conservation of large, threatened TM species for WBT may provide a protective umbrella to numerous co-occurring species (Smith *et al.* 2012). Future studies should investigate the effect of conserving WBT-attractant species on populations of co-occurring species.

The likelihood of being selected as a WBT-attractant species at a specific site may have been affected by the number of species present at the site. Wild boar (*Sus scrofa*) and common wart-hog (*Phacochoerus africanus*) share similar trait values. Both are in order artiodactyla with average body masses between 82-84 kg (Silva & Downing 1995). However, wild boar was mentioned 120 times whilst common wart-hog was only mentioned 37 times by the reviewed sources. Wild boar occurs in regions of relatively low TM species richness across Europe whilst common wart-hog occurs in species rich regions of East Africa (Figure 2.5). If wild boar shared the same geographic range as common wart-hog, wild boar may not have been mentioned by the sources as many times as the likelihood of more attractive TM species being present and mentioned instead would be greater. Conversely, marsh deer (*Blastocerus dichotomus)*, derby eland (*Taurotragus derbianus*) and Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*) occur in species rich regions of sub-Saharan Africa and were over-predicted by the best fitting model of TM-IOA, receiving residual values of 21.98, 21,49 and 20.91, respectively (Table 2.8). If these three antelope species were present in areas of lower TM species richness, they may have been mentioned more frequently by the sources.

2.4.2 Range Size

Range size was also identified as a significant factor, responsible for explaining variation in TM species attractiveness values (Tables 2.5 & 2.6). Previous studies suggest TM species, endemic to specific biogeographical or political regions, are more attractive to WB-tourists than widespread species (Williams *et al*. 2000; Veríssimo *et al.* 2009). Yet, both models in this study predict that TM species with larger range sizes are more attractive to WB-tourists than restricted range species (Figure 2.3D). This finding may be an artefact of the method used for deriving TM-IOA. The total number of times a TM species was selected by the sources was used

as its TM-IOA value. However, widespread species are present in a greater number of the PAs than restricted range species and hence are more likely to be mentioned by the sources across multiple sites than restricted range species. For example, both African bush elephant (*Loxodonta africana)* and Bornean orangutan (*Pongo pygmaeus)* were referenced by all of the reviewed sources. However, on average, African bush elephant was referenced 13.76 times per source, whilst Bornean orangutan was referenced only 1.76 times per source. African bush elephant may have a higher TM-IOA value because it is more attractive to WB-tourists, or because it is present in a greater number of PAs than the Bornean orangutan (African bush elephant is relatively widespread, with a range size of 2122 terrestrial grid cells, and was mentioned in association with 125 different PAs, whilst Bornean orangutan has a more restricted range size of 124 terrestrial grid cells, and was only mentioned in association with 12 PAs). Additional work is required to establish whether TM species with larger range sizes are more attractive to WB-tourists than restricted range species, or if this finding is an artefact of the method used for deriving TM-IOA. Future studies should control for the effect of the number of PAs containing a species by including it as a covariate in the model.

For the majority of TM species, mapped ranges are overestimates of locations where they truly occur as they generally correspond to extent of occurrence range maps, rather than area of occupancy (Somveille 2013). Future studies should use knowledge of TM species' habitat preferences, the distribution of remaining suitable habitat and species' elevation limitations, to improve estimates of TM species distributions (Somveille 2013). Furthermore, in this study analyses were conducted on the 2370 TM species, for which all trait data were available. However, there may have been a bias in which TM species data were available for. Additional trait data are required to ensure analyses provide a comprehensive assessment of the attractiveness of all TM species.

Care should be taken when drawing conclusions about the attractiveness of TM species assemblages from Figures 2.5-2.11 as the attractiveness of a TM species assemblage may vary, depending on the composition of TM species forming the assemblage. For example, assemblage A may be formed of ten TM species, each with a TM-IOA value of ten, whilst assemblage B may be formed of one TM species with a TM-IOA value 91 and nine TM species with a TM-IOA value of one. Despite having equal TM species richness and summed TM-IOA values, assemblage B may be more attractive to WB-tourists than assemblage A. Equally, assemblage C may be formed of only four TM species, but each TM species may have a TM-IOA value of 25. Despite having lower species richness than assemblages A and B, assemblage C may be more attractive to WB-tourists due to the presence of multiple large iconic species. In Chapter Three, I will test this hypothesis by comparing the effect of summed TM-IOA and species richness on protected area attractiveness.

Rather than using the summed TM-IOA values of all the TM species within each PA as the measure of PA attractiveness, future studies could consider how evenly distributed TM-IOA values are across the species within each PA. Alternatively, the average TM-IOA in each PA, or the TM-IOA of the most attractive species present in each PA, could be used as a measure of PA attractiveness.

2.4.3 Impact of Marketing on Species Attractiveness

Several studies have reported a skew in the use of large, threatened TM species in advertising WBT destinations, notable the 'Big Five' species in Africa: lion, leopard, white rhino, African bush elephant and African buffalo (Goodwin & Leader-Williams 2000; Clucas *et al*. 2008; Okello *et al*. 2008; Verissimo *et al*. 2011; Di Minin *et al*. 2012). Targets of conservation campaigns and promotions, such as the 'Big Five',

were often selected more times by the sources than predicted by the best fitting model of TM-IOA (Table 2.8). Tiger (*Panthera tigris*) and giant panda (*Ailuropoda melanoleuca*), two popular flagship species, were also under-predicted by the best fitting model of TM-IOA, receiving residual values of -54.56 and -10.22, respectively. This suggests that advertising may have a significant impact on the perceived attractiveness of TM species to WB-tourists (Maciejewski & Kerley 2014). Changes in marketing and improvements in public knowledge and awareness of a wider range of species could help reduce preferences for large TM species, directing pressure away from 'popular' WBT destinations and towards areas that lack charismatic megafauna (Thirgood *et al*. 2006; Di Minin *et al*. 2012).

2.4.4 Regions with High Wildlife-Based Tourism Potential

Southern and eastern African savannahs were allocated the highest TM species richness (Figure 2.5), summed TM-LOS (Figure 2.8) and summed TM-IOA (Figure 2.9) values, suggesting that these regions may be priority sites for WBT (Maciejewski & Kerley 2014). Sub-Saharan Africa is already home to some of the most well-known and successful WBT destinations worldwide (Higginbottom *et al.* 2005). For example, Serengeti National Park and Ngorongoro Conservation areas in Tanzania, which generate approximated US$5.2 and US$5.9 million per year from WBT, respectively (Thirgood *et al*. 2006). Open savannah plains make it easy for WB-tourists to find and observe the high diversity and abundance of large TM species present in these regions (Higginbottom *et al.* 2005), whilst numerous ungulate-predator combinations provide WB-tourists with increased opportunities to observe predation activities (Lindsey *et al*. 2007).

2.4.5 Regions with High Potential that are currently Underexploited

The Amazon, Congo basin (West Africa) and Indochina were highlighted as regions of high TM species attractiveness, both in terms of summed TM-LOS (Figure 2.10) and TM-IOA (Figure 2.11), based on the presence of false positive WBT-attractant species (defined as TM species in Figure 2.1, quadrant A). These regions could be seen as areas of lost or overlooked WBT potential and may be underexploited due to their relative inaccessibility, politically instability, shortages of capital and expertise, and/or due to the dense forest habitats that dominate these regions (Thouless 2005).

A large degree of overlap was observed between the regions highlighted in Figure 2.11 and regions identified by previous studies as target sites for proactive conservation, based on their 'low vulnerability (threat) and high irreplaceability' (Brooks *et al*. 2006; Mitterneier *et al*. 2003; Bryant *et al*. 1997; Sanderson *et al.* 2002). Opportunities for biodiversity conservation in the highlighted regions, specifically in the three major tropical rainforests of Amazonia, the Congo and New Guinea, may be considerable (Cardillo *et al*. 2006; Marco *et al.* 2016). However, forest environments are notoriously difficult for wildlife viewing as species are well concealed in dense foliage (Goodwin & Leader-Williams 2000; Kiss 2004; Maciejewski & Kerley 2014). The most desirable habitats for wildlife watching are open, allowing good visibility of a wide range of attractive species (Kerley *et al.* 2003). This may help explain (1) why densely forested regions of the Amazon, Congo basin and Indochina remain underexploited, and (2) the large discrepancy in the number of times African forest elephant and African bush elephant were mentioned by the sources. African forest elephant and African bush elephant share similar trait values; both species are large, threatened, diurnal herbivores, in order Proboscidea. However, African bush elephant was mentioned 234 times by the sources, whilst African forest elephant was only mentioned 35 times. African bush elephant occurs in open environments, where

it is easier for WB-tourists to observe the species, whilst African forest elephant occurs in densely forested environments.

The political stability of a species' range may also be important in explaining variation in the number of times a TM species is mentioned (TM-IOA). Both eastern gorilla (*Gorilla beringei*) and western gorilla (*Gorilla gorilla*) are patchily distributed, with relatively restricted ranges yet, eastern gorilla was mentioned 35 times, whilst western gorilla was only mentioned 19 times. Western gorilla occurs in politically unstable regions of the Congo basin, whilst eastern gorilla occurs in regions of Uganda, which are more politically stable (World Governance Indicators 2016). In addition, the attractiveness of a TM species to WB-tourists may depend on the species' population density (species per unit area) and/or migratory tendency. TM species that live in large groups and/or at relatively high densities, such as blue wildebeest (*Connochaetes taurinus*), may be more attractive to WB-tourists as they are easier to observe than solitary species, such as the snow leopard (*Uncia uncia*). Future studies should obtain information on primary habitat association, population density and migratory tendency, as well as the political stability of a species' range, for all TM species, and use these variables as additional modifiers of TM-IOA.

2.4.6 Regions with Low Wildlife-Based Tourism Potential

The Caribbean, Madagascar and Australasia were identified as regions of relatively low TM species attractiveness (both in terms of summed TM-LOS and TM-IOA), compared to other regions of the world (Figures 2.8 & 2.9). This finding may be an artefact of the sources and methods used for deriving TM-LOS and TM-IOA values, or due to additional variables that were not included in the modelling framework. WB-tourists are often drawn to Madagascar, Australasia and other island countries by the existence of high levels of endemism and non-TM species (Valentine & Birtles 2008). WBT destinations in Australia, for example, often have a primary focus on marine animals, including whales, dolphins and coral reef organisms, whilst sites in New Zealand and the Caribbean are more commonly advertised in association with bird species, rather than TM species (Home *et al.* 2009). However, neither endemism, nor the presence of non-TM species, were included as explanatory variables in the modelling framework. In addition, WBT destinations in Madagascar were frequently advertised in association with lemurs (Valentine & Birtles 2008). However, references were rarely made to individual species of lemur. In this study, references made to high orders of classification, such as 'lemur', were recorded in the database but were excluded from subsequent analyses; only references made to individual species were included, which may help explain why Madagascar was not identified as a hotspot for WBT. Furthermore, the majority of sources used to estimate TM species attractiveness were published by UK based companies (Table 2.3). Assuming their primary consumers are also UK based, the time and financial cost associated with travelling from the UK to the Caribbean, Madagascar and Australasia may help explain why these more remote destinations were identified as regions of relatively low attractiveness.

2.4.7 Limitations and Recommendations

The sources used to estimate TM species attractiveness were written over a period of 20 years, during which time WBT activities and preferences may have changed, with changes in political stability, accessibility, economic and WBT development. The authors may have used earlier sources as references, so each source might not have been independent. Furthermore, the majority of sources used were published by UK based companies, which may have affected the likelihood of a specific species being selected as a WBT-attractant species at a specific site (Table 2.3). Future studies could use the 'travel cost method' (TCM) as an alternative measure of TM species attractiveness. TCM is one of the oldest and most popular environmental valuation techniques (Hotelling 1947; Clawson 1959; Knetsch 1963; Hanley *et al.* 2001). It is based on the theory that the more time and money a person has spent travelling to see a site, or species, the higher they value it (Herath & Kennedy 2004). Future studies could collect information on where WB-tourists at each site had travelled from, the length of time and the amount of money they spent at each site, and which species they travelled to see. The cumulative time, distance travelled and money spent by visitors to see each species could then be used as alternative measures of species attractiveness. Alternatively, TM species attractiveness could be quantified using collections in zoos, or using photographs uploaded by WB-tourists onto online social media websites, such as flickr, Instagram and Facebook (Wood *et al*. 2013).

2.5 CONCLUSION

In this study, I have identified species that act as WBT attractants, and the traits that lead to such species being attractive to WB-tourists. I have allocated TM attractiveness values to all TM species, for which all trait data were available. I used these values to identify areas with high TM species assemblage attractiveness (Figure 2.9), and regions with high WBT potential, based on the attractiveness of the TM species assemblages present, that are currently underexploited (Figures 2.10 and 2.11).

In the next chapter, I will consider which additional features of PAs make them attractive to WBT. If TM species are not important in predicting PA attractiveness, the future loss of TM species from PAs may have little influence on their future cultural services. Conversely, if TM species are key in attracting WB-tourists to PAs, greater investment in TM species conservation would be beneficial in maintaining and enhancing PA attractiveness to WB-tourists.

Chapter 3: Which features of protected areas make them attractive to wildlife-based tourists?

3.1 INTRODUCTION

Protected areas (PAs) are defined by the International Union for the Conservation of Nature (IUCN) as: *"clearly defined geographical spaces, recognised, dedicated and managed, through legal or other effective means, to achieve the long term conservation of nature, with associated ecosystem services and cultural value"* (Dudley 2008). PAs now cover more than 15% of the Earth's land area (UNEP-WCMC 2014), and play an important role in conservation, education, recreation and research (Clius *et al*. 2014). They host the majority of wildlife-based tourism (WBT) activities worldwide (Balmford *et al.* 2015) and are commonly recognised as our most important unit for *in situ* conservation (Chape 2005).

The IUCN group PAs into seven broad categories, based on their primary management objectives (Table 3.1). Management categories are internationally recognised and facilitate a global system for defining, recording and classing PAs (Dudley 2013). PAs in management category Ia (strict nature reserves) are managed primarily for scientific research and environmental monitoring, whilst PAs in management category VI (natural resource PAs) are mostly unmodified natural habitats, managed with both the protection of biodiversity and the provision of resources to local communities in mind (IUCN 2016; Table 3.1). At present, 66% of PAs listed in the World Database of Protected Areas (WDPA) are categorised. Management categories for the remaining 34% of PAs have either not been assigned, not been reported or are not applicable (IUCN 2016). In this study, PAs will be defined as those which fall into management categories Ia to VI (Table 3.1).

Table 3.1: Protected area management category definitions (IUCN 2016).

Management Category	Description
Ia	Strict Nature Reserves (protected from all but light human use)
Ib	Wilderness Areas (human use is limited)
II	National Parks (human visitation is allowed)
III	Natural Monument or Feature (human visitation is allowed)
IV	Habitat/Species Management Area (human visitation is allowed)
V	Protected Landscape/Seascape (human visitation is allowed)
VI	Protected Area with Sustainable Use of Natural Resources (human visitation is allowed)

WBT is any form of tourism that is based on visitors encountering wildlife (Higginbottom & Tribe 2005). It is capable of generating substantial revenue for both local economies and conservation (Dharmaratne *et al*. 2000; Lindsey *et al*. 2007; Bayliss *et al*. 2014), and provides important justification for the continued existence of PAs, as they come under increasing pressure for land to be put to alternative, not conservation uses, such as agriculture and mining (Balmford *et al.* 2015). Yet, the principal factors that drive wildlife-based (WB) tourists to visit specific PAs remain poorly understood. A greater understanding of these factors would enable us to highlight PAs, with high WBT potential, that are currently underexploited. This could have significant benefits for wildlife conservation and socioeconomic development in the highlighted regions (Bayliss *et al*. 2014).

3.1.1 Primary Attractants of Protected Areas

Table 3.2 summarises the primary attractants of WBT destinations, mentioned by previous studies. These include: human factors (such as sanitation, security, land status and accessibility), natural resource factors (such as flora, fauna and cultural heritage) and biophysical factors (such as landforms and climatic phenomena).

Table 3.2: Primary attractants of wildlife-based tourism (WBT) destinations, as evaluated in previous studies.

Key factors that contribute to the perceived attractiveness of WBT destinations	**Source**
Park area, local population size, remoteness, natural attractiveness, national income	Balmford *et al.* (2015)
Recreational opportunities, number of biotopes, the provision of trails, park age, location	Neuvonen *et al*. (2010)
Attractive scenery, high bird diversity, high mammal diversity, high floral diversity, large predators	Lindsey *et al.* (2007)
Climate (temperature and rainfall), vegetation, and tourist resources	Richardson & Loomis (2005)
Climate, safety, political stability, infrastructure, accessibility, diversity of wildlife, abundance of wildlife, size and quality of PA system, availability of relatively undisturbed natural areas	Higginbottom & Buckley (2003)
Quality of wildlife, security, infrastructure	Akama & Kieti (2003)
Tourist resources, tourist facilities, accessibility, local communities, peripheral attractions	Deng *et al.* (2002)
Location, distance from population centres, recreational facilities, park area, uniqueness	Hanink & Stutts (2002)
Mammalian diversity, large predators, mega-herbivores	Walpole & Leader-Williams (2002)
Tourism resources , regional conditions, peripheral conditions	Bao & Chu (1999)
Resource value, scenic attributes, tourism conditions	Yang (1994)
Mountains, water, forest environment, wildlife, plants, cultural heritage, landscape	Wu, Li & Deng (1992)
Infrastructure, access, political stability, marketing, spectacular natural features, readily visible natural features	Wells (1992)
Landforms, climate, vegetation, land status, accessibility, wildlife, visual resources, local recreational use, cultural heritage	Ethos Consulting (1991)
Structural differentiation, infrastructure	Mills & Westover (1987)

The overall attractiveness of a WBT destination to a WB-tourist may depend on its tourist resources, tourist facilities, accessibility, local communities and peripheral attractions (Deng *et al.* 2002); it's size (Balmford *et al.* 2015), habitat diversity (Neuvonen *et al*. 2010), abundance and charisma of wildlife (Higginbottom & Buckley 2003; Loureiro *et al.* 2012), temperature (Richardson & Loomis 2005), availability of infrastructure and cultural attractions (Wood *et al*. 2013; Mills & Westover 1987) and/or the political stability of the region, within which the WBT destination resides (Akama & Kieti 2003). It has been suggested that, for example, the rapid development and expansion of WBT operations in Kenyan PAs during the 1970's and 1980's was due to the country's economic and political stability, relative to neighbouring countries that were experiencing political turmoil and civil unrest (Akama & Kieti 2003). Over the past few decades, however, Kenya has been perceived as an increasingly insecure destination, whilst the socio-political situations in Tanzania and Uganda have improved significantly, which may help explain their increased success as WBT destinations (World Bank 2016). In Tanzania, for example, the recorded number of international visitors increased by 56%, between 2000 and 2010, from 501,000 to 782,000 (Bayliss *et al.* 2014). Tourism increased its contribution to Tanzanian gross domestic product (GDP) during this same period, from US$615 million to US$1.75 billion (Mitchell *et al.* 2009).

3.1.2 Protected Area Visitation Rates

Several studies have considered how features of PAs affect annual visitation rates (Loomis *et al.* 1999; Hanink & Stutts 2002; Loomis 2004; Ejstrud 2007; Neuvonen *et al.* 2010; Balmford *et al.* 2015). Balmford *et al.* (2015) built a modelling framework to predict PA visitation rates, based on PA size, local population size, remoteness, national income and natural attractiveness. The authors found that larger, less remote PAs, in countries with higher national incomes, have higher visitation rates

than smaller, more remote PAs, in countries with lower national incomes (Balmford *et al.* 2015). Others have found that the number of visits a PA receives depends on its location, relative to the population of potential users (Hanink & Stutts 2002), and/or its age (Neuvonen *et al.* 2010). Older PAs may have higher visitation rates than more newly established PAs due to greater public awareness of older PAs, or, because the most attractive destinations were protected first and their services are better developed (Mills & Westover 1987; Neuvonen *et al.* 2010).

Modelling PA visitation rates enables park owners to predict the effect of management decisions on the number visitors to a PA, as well as the socioeconomic impacts of such decisions (Neuvonen *et al.* 2010). This information is essential in planning and managing existing PAs, and in establishing new PAs. However, visitation rate data for PAs worldwide is limited, particularly for island states and across much of the Middle East and North Africa (Waldron *et al.* 2013; Amano & Sutherland 2013), and the methods used for deriving visitation rates vary considerable across PAs (Balmford *et al*. 2015). Some use gate receipts and road counts, and consider multiple-day or multiple-entry passes as single visits, whilst others use automated trail counts, and report visitation rates as the number of people entering the PA each day (Eagles 2003; Cessford & Burns 2008). Furthermore, visitation rates provide no indication of the motivations of tourists for visiting PAs. Some tourists may visit specific PAs in order to participate in physical activities, such as canoeing or mountain-biking, whilst others may visit specific PAs to participate in observational activities, such as wildlife-watching. Visitation rates are, therefore, limited in their ability to predict the attractiveness of global PAs to WB-tourists, specifically WB-tourists with terrestrial mammal (TM) species viewing preferences. In this study, I adopt an alternative method for quantifying the attractiveness of PAs to WB-tourists. I extract data on PAs mentioned within a range of WBT guidebooks, travel brochures and online resources, all of which are global in scope. I use the number of sources that mention a PA as

the PA's index-of-attractiveness (PA-IOA) and build a modelling framework to predict PA-IOA, based on a range of biophysical and socioeconomic variables. I use the model to identify PAs with high WBT potential that are currently underexploited. I investigate the correlation between predicted PA-IOA values and PA visitation rates to determine whether (or not) the model can be used to estimate the number of people (i.e. not just WB-tourists) that visit PAs worldwide.

I include wildlife attractiveness as an explanatory variable in my modelling framework. Previous studies have intersected PA shapefiles from the WDPA with: biome-realm shapefiles, to assign natural attractiveness scores to PAs worldwide (Balmford *et al.* 2015); and with terrestrial (Rodrigues *et al.* 2015) and marine (Klein *et al*. 2015) species' mapped distributions, to assess the representation of biodiversity in terrestrial and marine PAs, respectively. Others have used species' distribution maps to assess the effect of habitat loss and degradation on amphibian (Ficetola *et al.* 2015) and bird (Harris & Pimm 2004; Schell *et al.* 2013) species.

In this study, I intersect PA shapefiles with species' distribution maps to predict species lists for PAs worldwide. I use these lists to assign wildlife attractiveness scores to global PAs. Species' distribution maps provide a simple and data-inexpensive approach for summarising species' distributions (Somveille 2013). However, for the majority of species mapped ranges are overestimates of locations where they truly occur, as they generally correspond to extent of occurrence, rather than area of occupancy (Somveille 2013). Consequently, species may be listed as present in PAs where they do not occur, or listed as absent in PAs where they do (Townsend 2016). I validate the PA shapefile intersection method using actual species lists for a subset of global PAs (Niwattanakul *et al.* 2013).

3.2 METHODS

3.2.1 Data Collection

I downloaded the WDPA dataset from ProtectedPlanet (2016). WDPA contains information on 144,318 PAs, in management categories Ia to VI, including data on PA size and location. In this study, I concentrated on a subset of 48,715 terrestrial PAs, with polygon data available and an area exceeding 1 km^2 (Table 3.3). WDPA classifies PAs as being (a) completely within the terrestrial and/or freshwater environments, (b) partially (coastal) within the marine environment (on the coast and encompassing part of the sea/ocean), or (c) completely within the marine environment (sea, ocean or equivalent), and provides PA spatial data in the form of boundaries (polygons) wherever it is available, or as a single latitude and longitude coordinate point, where boundary data is not available (WDPA 2016). Polygon data are available for 89% of PAs in the WDPA. The remaining 11% of PAs are only presented as points (Table 3.3). I focused on the subset of PAs, completely within the terrestrial and/or freshwater environments, and excluded PAs presented only as a point from further analyses (Table 3.3). Most estimates of the minimum area needed to support intact communities of vertebrate species are significantly larger than 1 km^2 (Gurd *et al.* 2001). I excluded PAs with areas below 1 km^2 as these are unlikely to support assemblages of large TM species, and subsequently attract WB-tourists with large TM species viewing preferences.

I compiled a database of all the PAs mentioned by all available WBT guidebooks, travel brochures and online resources, with comprehensive global coverage, published within the past 20 years (Table 2.3). Each time that a PA was mentioned in one of the sources, in association with a TM species, the PA was recorded. The

total number of sources that mentioned a PA, in association with a TM species, was used as the PA's index of attractiveness (PA-IOA).

All sources were targeted at relatively inexperienced WB-tourists with broad wildlife viewing interests, and provide readers with advice on which wildlife species to see, where and when. WBT books often focus on PAs targeted by the mass WBT market, whilst online resources can include details for less developed sites. Using a diversity of sources ensured data were collected across a wide range of PAs, rather than focusing on just the most attractive sites.

There are many spatially overlapping PAs in the WDPA, with different management categories or designations (IUCN 2016). The same geographical area might be a 'National Park' under national legislation and a 'World Heritage Site' or 'Ramsar Site', under international agreements. For example, Yellowstone National Park, USA, is classified as both a National Park and a natural World Heritage Site in the WDPA (WDPA 2016). When PAs with multiple designations were mentioned by the sources, the designation with the lowest management category classification was selected.

For each of the 48,715 PAs of interest, I derived eight variables which I hypothesised would help explain variation in PA-IOA (Table 3.4). These variables include: PA size, management category, accessibility, location and wildlife attractiveness; as well as the national income, political stability and spoken language of the country in which each PA resides. I extracted PA size, management category and location (in terms of which continent the PA is on) data, for all 48,715 PAs of interest, from the WDPA online database (Table 3.4).

Table 3.3: Number of terrestrial protected areas (PAs), with polygon data available and an area greater than 1 km^2, in each management category, mentioned by the sources and included in this study.

Management Category	Number of PAs	Number of terrestrial PAs	Number of PAs with polygon data available	Number of PAs with area greater than 1 km^2	Number of PAs included in this study	Number of PAs mentioned by the sources
Ia	11,271	9,818	11,135	5,073	4,485	44
Ib	2,988	2,780	2,988	2,397	2,254	28
II	5,346	4,548	5,208	4,602	3,996	281
III	25,280	24,328	14,515	4,058	3,754	14
IV	59,199	55,760	56,482	21,258	19,361	74
V	32,721	30,407	31,191	13,105	11,795	63
VI	7,513	6,195	7,352	4,055	3,070	32
Total	144,318	133,836	128,871	54,548	48,715	536

Table 3.4: List of the eight variables, used to explain variation in protected area (PA) attractiveness, and the sources from which they were derived.

Variables	Source
PA Size	WDPA (available at: http://www.protectedplanet.net/)
Management Category	WDPA (available at: http://www.protectedplanet.net/)
Continent	WDPA (available at: http://www.protectedplanet.net/)
National Income	World Bank (available at: http://info.worldbank.org/)
Accessibility	WDPA (available at: http://www.protectedplanet.net/) OpenFlights (available at: http://openflights.org/data.html)
Political Stability	World Bank (available at: http://info.worldbank.org/)
Spoken English Category	Melitz and Toubal (2016)
Wildlife Attractiveness	Chapter Two

I downloaded PA polygon data from the WDPA (2016) and x-y coordinate information for 8107 airports worldwide, from the OpenFlights online database (Table 3.4). I measured the shortest straight-line distance from each PA polygon perimeter to the x-y coordinates of its closest international airport, using the 'rgeos' package in R (R Development Core Team 2016). I used the distance to a PA from its closest international airport as an estimate of the PA's accessibility.

Each year, the World Bank Group provide GDP per capita values, and political stability scores, for each country of world (World Bank 2016). GDP per capita is calculated by dividing GDP by mid-year population size (World Bank 2016). It measures the gross value added by all resident producers in the economy (World Bank 2016). Meanwhile, political stability scores reflect perceptions of a countries' likelihood of political instability and/or politically-motivated violence, including terrorism (Worldwide Governance 2016). The WBT guidebooks, travel brochures and online resources, used to derive PA-IOA values, were published between 1996 and

2016 (Table 2.3). I calculated average national income (GDP per capita) and political stability scores, using data published by the World Bank Group (2016), across the same twenty year period, for each country of the world. I assigned average national income and political stability scores to each PA according to the country in which the PA resides.

Most of the sources used to derive PA-IOA values were targeted at English speaking WB-tourists (Table 2.3). I hypothesised that English speaking WB-tourists would be more attracted to PAs in countries with English as an official language than countries where English is not spoken. Melitz and Toubal (2016) produced a database of languages spoken in 195 countries. I used the database to categorise each country of the world, according to whether (or not) English is (a) the country's official language, (b) spoken in the country as one of many languages, or (c) not spoken in the country (Melitz & Toubal 2016). I assigned a 'spoken English' category to each PA according to the country in which the PA resides.

Next, I estimated the wildlife attractiveness of each PA. In Chapter Two, I allocated attractiveness values to all TM species. If TM species lists had been available for all PAs worldwide then I would have summed together the attractiveness values of all the TM species on a PA's species list and used this as an estimate of the site's wildlife attractiveness. Unfortunately, however, TM species lists are only available for a limited number of PAs (Balmford *et al.* 2015). To overcome this issue, I predicted TM species lists for global PAs by overlaying PA and TM species polygon data, downloaded from the WDPA (2016) and IUCN (2016) online databases, respectively, in R (R Development Core Team 2016). If a TM species' polygon intercepted a PA polygon it was included on the species list for that PA.

In order to test the reliability of this PA polygon overlay method, I compiled actual TM species lists for 86 PAs worldwide, using a variety of sources (Table 3.5), and measured the similarity between the actual and predicted TM species lists using the Jaccard similarity coefficient (Niwattanakul *et al.* 2013).

Equation 3.1:
$$Jaccard\ Similarity\ Coefficient(A,B) = \frac{|A \cap B|}{|A \cup B|}$$

The Jaccard similarity coefficient, defined as the size of the intersection divided by the size of the union between two data sets, is a statistic used for comparing the similarly between two data sets (Niwattanakul *et al.* 2013). In Equation 3.1 the intersection between two sets (A and B) is denoted A∩B and reveals all items which are in both sets, whilst the union between two sets (A and B) is denoted A∪B and reveals all items which are in either set (Niwattanakul *et al.* 2013). The Jaccard similarity coefficient for two identical data sets is equal to one, whilst the Jaccard similarity coefficient for two mutually exclusive data sets is equal to zero.

Table 3.5 List of sources used to compile terrestrial mammal species lists for protected areas.

Source	Web Links
National Parks and Wildlife Service	www.nationalparks.nsw.gov.au/
National Parks of East Africa (Williams *et al.* 1994)	Not applicable
National Park Service	www.nps.gov/
National Parks Worldwide	www.nationalparksworldwide.com/
Parks and Wildlife Service	www.parks.tas.gov.au/
Parks Australia	www.parksaustralia.gov.au/
South African National Parks	www.sanparks.org/
Thai National Parks	www.thainationalparks.com/

In Chapter Two, a significant correlation was found between regions with high TM species assemblage attractiveness and high TM species richness (Figures 2.5 & 2.9). In order to determine which is more important in predicting PA-IOA, I compared two similar models: the first included TM species assemblage attractiveness as the measure of wildlife attractiveness, calculated by summing together the attractiveness values of all the TM species on a PA's predicted species list, whilst the second included TM species richness as the measure of wildlife attractiveness, defined as the number of TM species on a PA's predicted species list. In a third model, I considered TM species threat status as an alternative measure of wildlife attractiveness, defined as the number of TM species, in IUCN Red List status categories: vulnerable, endangered or critically endangered, on a PA's predicted species list (IUCN 2016).

Balmford *et al.* (2015) produced a database of visitor records to PAs worldwide. I used the database to calculate mean annual visitation rates for 302 PAs, across 39 countries. 113 (37.4%) of these PAs were selected by at least one of the reviewed sources (Table 2.3), and were subsequently allocated PA-IOA values greater than zero. I performed linear regression analyses to compare mean annual PA visitation rates with actual PA-IOA values, derived from the sources, and predicted PA-IOA values derived from the best fitting model of PA-IOA, in order to determine whether (or not) the best fitting model of PA-IOA could be used to estimate the number of people, i.e. not just WB-tourists, that visit PAs worldwide.

3.2.2 Statistical Analysis

In this study, I focused on 48,715 terrestrial PAs with polygon data available, in management categories Ia to VI, and with an area exceeding 1 km^2 (Table 3.2). Only 536 (1.10%) of these PAs were selected by at least one of the reviewed sources

(Table 2.3), and were subsequently allocated PA-IOA values greater than zero. To account for zero-inflation and over-dispersion in the PA-IOA dataset, two separate analyses were performed. First, a binary generalised linear model (GLM) was used to predict whether PAs were mentioned (or not) by the sources (hereafter referred to as a PA's likelihood-of-selection, or PA-LOS), using the 'MASS' package in R (R Development Core Team 2015). The binary GLM was fitted to 1,000 bootstrapped replicates of the data, using the 'boot' package in R (Efron & Tibshirani 1991; R Development Core Team 2015). Each replicate included all 536 PAs that were selected by at least one of the sources, as well as a randomly stratified sample of 536 PAs that were not selected by any of the sources. Random sampling, stratified within continents and across management categories, was used to produce replicates of the 536 PAs that were selected by the sources (i.e. 536 PAs that were allocated PA-IOA values of zero were drawn at random to replicate the spatial distribution and management categories of the 536 PAs that were selected by at least one of the sources), to ensure a representative spread of data. Second, a negative binomial GLM was used to predict PA-IOA values (i.e. the total number of sources that mentioned a PA) for the 536 PAs that were selected by at least one of the sources, using the 'MASS' package in R (R Development Core Team 2015). Both models included as explanatory variables: PA size, management category, accessibility, national income, political stability, 'spoken English' category, continent and a measure of wildlife attractiveness (TM species: assemblage attractiveness, richness or threat status). Models were initially run with interaction terms included. However, interaction terms were not found to be significant, so were removed from subsequent models.

To avoid selecting overly complex models I used model selection, applying a two-step selection criterion (following Richards 2008) to evaluate the top candidate models. I initially retained models if they had a delta Akaike Information Criterion

(∆AIC) within six units of the model of best fit (Richards 2008). To remove overly complex models I disregarded models with a higher AIC value than any simpler nested models. Analyses were repeated three times; each time a different measure of wildlife attractiveness was included in the modelling framework. I compared the AIC values of each model, to determine which measure of wildlife attractiveness is more important in predicting PA-IOA.

To explore the effect of variation in single parameters on a PA's (1) likelihood-of-selection (PA-LOS), and (2) index-of-attractiveness (PA-IOA), I sequentially varied individual parameters in both the best binary GLM (for PA-LOS) and the best negative binomial GLM (for PA-IOA), whilst holding all other parameters in the model at a fixed value. The fixed parameter dataset was centred on the mean values for PAs: PA size (347.53 km^2), accessibility (54.26 km), national income (2.99), political stability (0.65), spoken English category (English spoken as one-of-many languages), management category (National Parks), continent (North America) and wildlife attractiveness (TM species: assemblage attractiveness: 279.00; species richness: 29.87; threat status: 19.26).

The binary GLM produced probabilistic predictions. In order to evaluate the model's ability to predict whether (or not) a PA was mentioned by at least one of the sources, I applied an optimal threshold value to convert the probabilistic predictions into the original binary format (Guisan & Zimmermann 2000; Allouche *et al.* 2006). I used the maximum value of Cohen's kappa (k) as the threshold value to distinguish a subset of false positive and negative predictions (McHugh 2012). I used the area under the curve (AUC) of a receiver operating characteristic (ROC) plot to evaluate the accuracy of the binary GLM (Fielding & Bell 1997; Fielding 2002; Allouche *et al.* 2006). I defined AUC values of 0.8< as a null model, 0.8<AUC<0.9 as a fair model, 0.9<AUC<0.95 as a good model, and 0.95<AUC<1.00 as a very good model (Thuiller *et al.* 2006).

3.3 RESULTS

3.3.1 Predicting Protected Area Species Lists

The mean Jaccard similarity coefficient for actual and predict PA species lists was 0.619 ± 0.157 standard deviations (n = 86). This is relatively high compared to Jaccard similarity coefficients reported in other studies (Makarova *et al*. 2013; Watanabe 2012). No correlation was found between Jaccard similarity coefficient and logged PA size (Linear Regression; $F_{1,84}$ = 1.649, P = 0.202; Adjusted R^2 = 0.0076), suggesting that there is no difference in the PA polygon overlay method's ability to predict TM species lists for PAs of differing sizes (Figure 3.1).

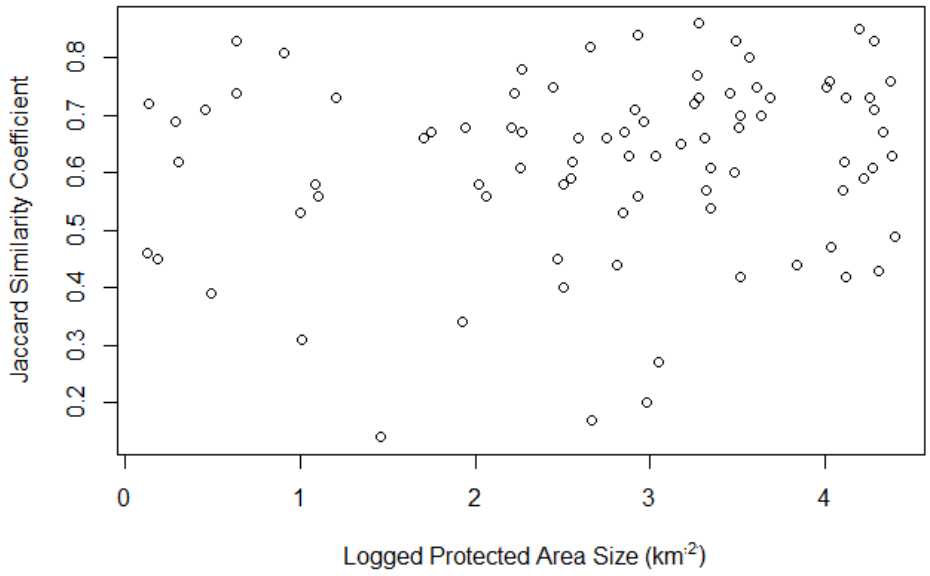


Figure 3.1: Jaccard similarity coefficients for protected areas worldwide, as a function of logged protected area size (n = 86).

The Jaccard similarity coefficients in this study were higher for North American, Kenyan and Tanzanian PAs than they were for South American and Asian PAs. For example Iguazú National Park, Argentina, received a Jaccard similarity coefficient of 0.015, whilst Denali National Park, Alaska, received a Jaccard similarity coefficient of 0.854.

3.3.2 Predicting Protected Area Likelihood-of-Selection

Model selection yielded two candidate binary GLMs with TM species richness as the measure of wildlife attractiveness, two candidate binary GLMs with TM species threat status as the measure of wildlife attractiveness, and three candidate binary GLMs with TM species assemblage attractiveness as the measure of wildlife attractiveness (Table 3.6). The best binary GLM explained 55.1% of the observed variation in PA-LOS (Table 3.6), and was considered a good model, with an AUC of 0.93 (Figure 3.2).

In the best binary GLM: both PA size (Figure 3.3A) and wildlife attractiveness (Figure 3.3B) were positively related to PA-LOS; accessibility (in terms of the distance to a PA from its closest international airport) was negatively related to PA-LOS (Figure 3.3C); National Parks were significantly more likely to be selected as WBT destinations than PAs in other management categories (Table 3.7); and PAs in Australasia, Europe and North America were significantly less likely to be selected as WBT destinations than PAs in Africa (Table 3.7).

Table 3.6: Top candidate binary GLMs i.e. have ΔAIC values that are ≤6 (Richards 2008), for each measure of wildlife attractiveness (terrestrial mammal (TM) species: richness, threat status and assemblage attractiveness). Maximum log-likelihoods (LL), ΔAICs and R^2 values are shown for each model. Df is the degrees of freedom in a given model. (+) and (N/A) indicate which variables are included, or excluded, in each model, respectively. (*) indicates the best binary GLM.

Measure of Wildlife Attractiveness	Model Number	PA Size	National Income	Political Stability	Accessibility	Spoken English Category	Wildlife Attractiveness	Continent	Management Category	Df	LL	ΔAIC	R^2 Value
TM species richness	1	+	N/A	+	+	+	+	+	+	18	-384.687	0	0.518
	2	+	N/A	N/A	N/A	N/A	+	+	+	14	-390.231	2.831	0.511
TM species threat status	3	+	N/A	+	+	N/A	+	+	+	16	-386.822	0	0.517
	4	+	N/A	N/A	N/A	N/A	+	+	+	14	-390.059	2.352	0.509
TM species assemblage attractiveness	5 *	+	N/A	N/A	+	N/A	+	+	+	15	-389.548	0	0.551
	6	+	N/A	N/A	N/A	+	N/A	+	+	15	-394.19	3.087	0.537
	7	+	N/A	+	N/A	N/A	N/A	+	+	14	-395.288	3.223	0.524

Table 3.7: Relative importance of protected area (PA) variables in predicting whether (or not) a PA will be selected as a wildlife-based tourism destination, based on the best binary GLM's predictions. P values significant at 5% levels are shown.

	Effect Size	Standard Error	z value	P
Intercept (*Continent: Africa, Management Category: Ia*)	0.87	0.29	3.01	0.041
PA Size (logged)	0.76	0.05	5.16	<0.001
Accessibility	-0.01	0.01	-3.29	0.016
Wildlife Attractiveness	0.03	0.01	3.94	0.002
Continent				
Australasia	-1.62	0.73	-2.23	<0.001
Europe	-1.83	0.75	-2.59	0.011
North America	-2.03	0.77	-2.63	0.018
Management Category				
II (National Parks)	0.87	0.35	2.51	0.012

PAs in Figure 3.2 quadrants (B) and (D) were selected by at least one of the reviewed sources, whilst PAs in Figure 3.2 quadrants (A) and (C) were not selected by any of the reviewed sources. The maximum value of Cohen's kappa (0.475) was used as the threshold value, to distinguish a subset of false positive (quadrant A) and false negative (quadrant D) predictions, derived from the best binary GLM. PAs in Figure 3.2 quadrant (A) are hereafter referred to as 'false positive WBT destinations'.

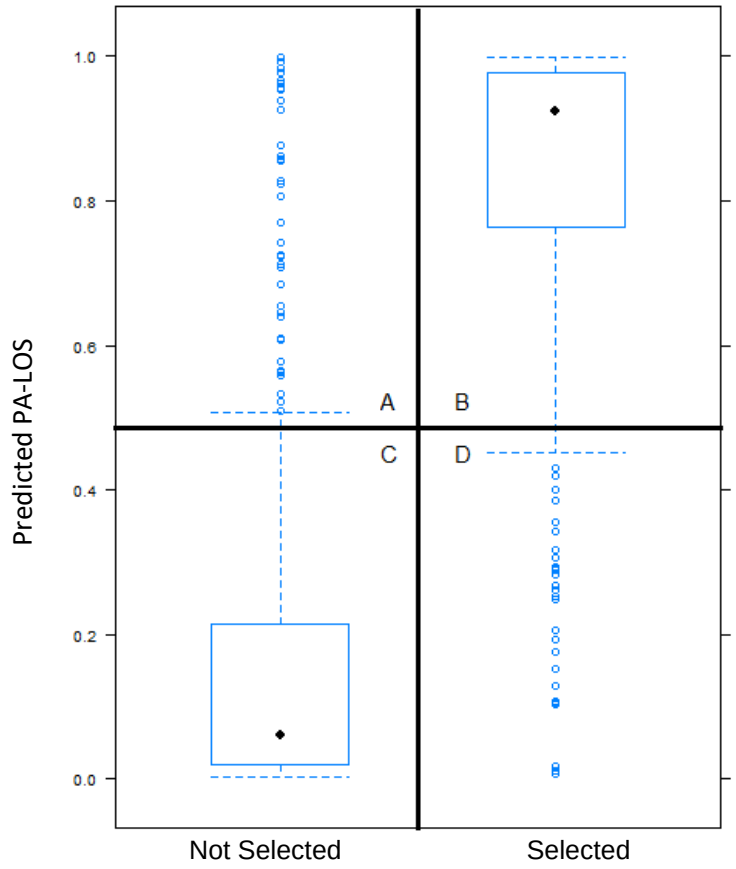
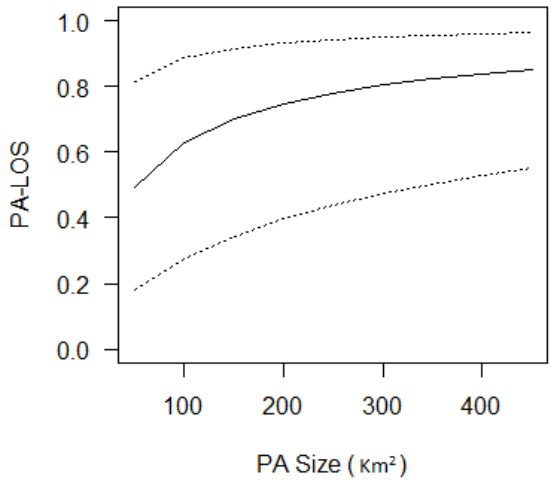
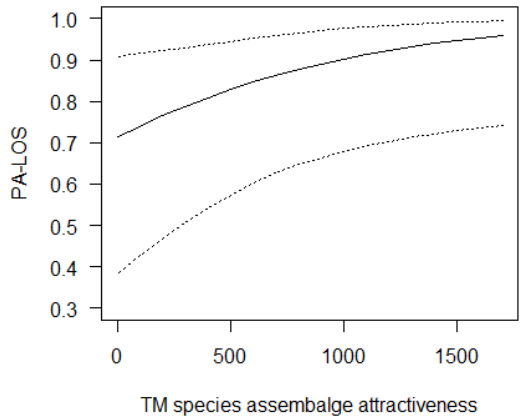


Figure 3.2: Boxplot compairson of protected areas (PAs) selected and not selected by the reviwed sources (x-axis) against their predicted likelihood of being selected (PA-LOS) as wildlife-based tourism (WBT) destinations, by the best binary GLM (y-axis). (A) False positive WBT destinations (B) True WBT destinations (C) Unattractive PAs (D) False Negative WBT destinations. AUC = 0.93 predicted (n = 48, 715).

A



B



C

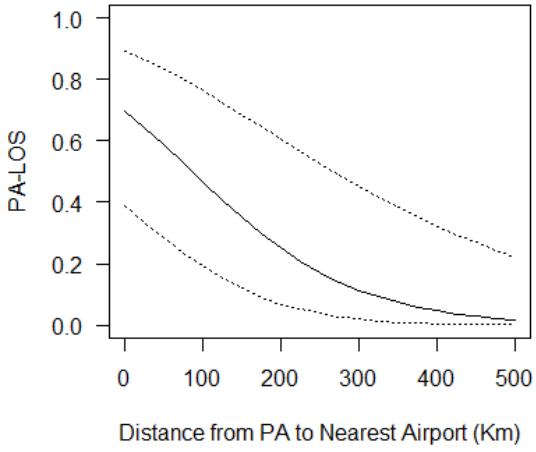


Figure 3.3: Effect of protected area (PA) (A) size, (B) terrestrial mammal (TM) species assemblage attractiveness, and (C) accessibility (in terms of the distance to a PA from it's closest international airport), on the likelihood of being selected as a wildlife-based tourism destination, by the best binary GLM. Solid lines represent the best binary GLM's predictions. Dashed lines represent ± 1 standard error (SE) of the mean.

3.3.3 Predicting Protected Area Index-of-Attractiveness

Model selection yielded two candidate negative binomial GLMs for each measure of wildlife attractiveness (Table 3.9). The best negative binomial GLM explained 28.7% of the observed variation in PA-IOA (Table 3.9). In the best negative binomial GLM: both PA size and wildlife attractiveness were positively related to PA-IOA; whilst accessibility (in terms of the distance to a PA from its closest international airport) was negatively related to PA-IOA (Table 3.8).

Table 3.8: Relative importance of protected area (PA) variables in predicting index-of-attractiveness (PA-IOA) based on the best negative binomial GLM's predictions. PA-IOA is defined as the number of reviewed sources that mention a PA. P values significant at 5% levels are shown.

	Effect Size	**Standard Error**	**z value**	**P**
Intercept	0.95	0.28	3.33	0.778
PA Size (logged)	0.30	0.07	4.21	<0.01
Wildlife Attractiveness	0.02	0.01	4.43	0.002
Accessibility	-0.01	0.01	-3.29	0.008

Table 3.9: Top candidate negative binomial GLMs i.e. have ΔAIC values that are ≤6 (Richards 2008), for each measure of wildlife attractiveness (terrestrial mammal (TM) species: richness, threat status and assemblage attractiveness). Maximum log-likelihoods (LL), ΔAICs and R^2 values are shown for each model. Df is the degrees of freedom in a given model. (+) and (N/A) indicate which variables are included or excluded in each model, respectively. (*) indicates the best negative binomial GLM.

Measure of Wildlife Attractiveness	Model Number	PA Size	National Income	Political Stability	Accessibility	Spoken English Category	Wildlife Attractiveness	Continent	Management Category	Df	LL	ΔAIC	R^2 Value
TM species richness	1	+	N/A	N/A	N/A	+	+	N/A	+	12	-918.749	0	0.263
	2	+	N/A	N/A	N/A	+	+	N/A	N/A	6	-926.673	3.402	0.271
TM species threat status	3	+	N/A	N/A	+	N/A	+	+	N/A	7	-1342.4	0	0.273
	4	+	N/A	N/A	N/A	+	+	N/A	N/A	6	-1342.63	0.073	0.269
TM species assemblage attractiveness	5	+	N/A	N/A	+	N/A	+	N/A	+	12	-918.042	0	0.275
	6 *	+	N/A	N/A	N/A	+	+	N/A	N/A	6	-925.937	3.346	0.287

A positive correlation was found between the actual and predicted PA-IOA values, by the best negative binomial GLM (Linear Regression; $F_{1,524} = 103.1$, $P < 0.01$; Adjusted $R^2 = 0.1628$). The adjusted R^2 value of 0.1628 is not very strong, indicating that the negative binomial GLM did not do well at predicting the number of sources that select each PA (Figure 3.4).

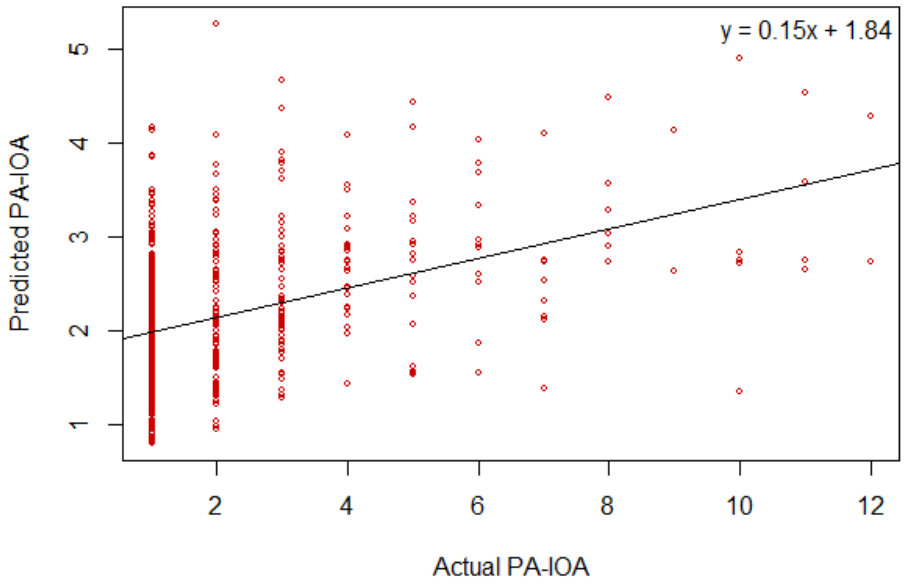


Figure 3.4: Actual and predicted protected area index-of-attractiveness (PA-IOA) values, derived from the best negative binomial GLM. PA-IOA is defined as the number of reviewed sources that mention each protected area. Significant linear regression line is shown. Adjusted $R^2 = 0.1628$ (n = 536).

3.3.4 Estimating Protected Area Visitation Rates

No correlation was found between visitation rates and actual PA-IOA values (Linear Regression; $F_{1,110} = 1.466$, $P = 0.229$; Adjusted $R^2 = 0.0042$), or visitation rates and predicted PA-IOA values (Linear Regression; $F_{1,299} = 1.052$, $P = 0.306$; Adjusted $R^2 = 0.0002$), suggesting that the best negative binomial GLM cannot be reliably used to estimate the number of people visiting PAs worldwide (Figure 3.6).

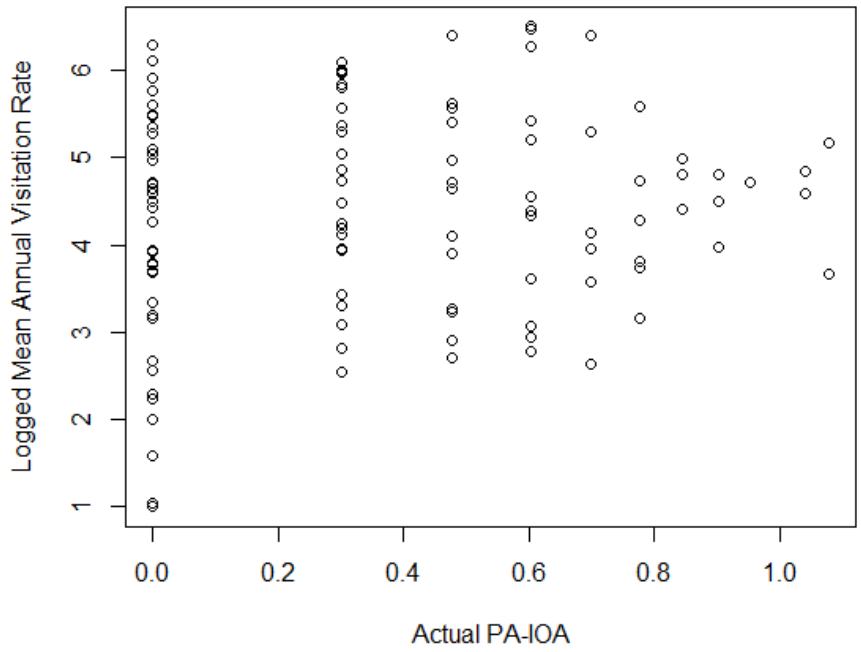


Figure 3.5: Mean annual visitation rates (logged) for protected areas that were selected by at least one of the sources, as a function of the number of times each protected area was selected by the reviewed sources (PA-IOA) (n = 113).

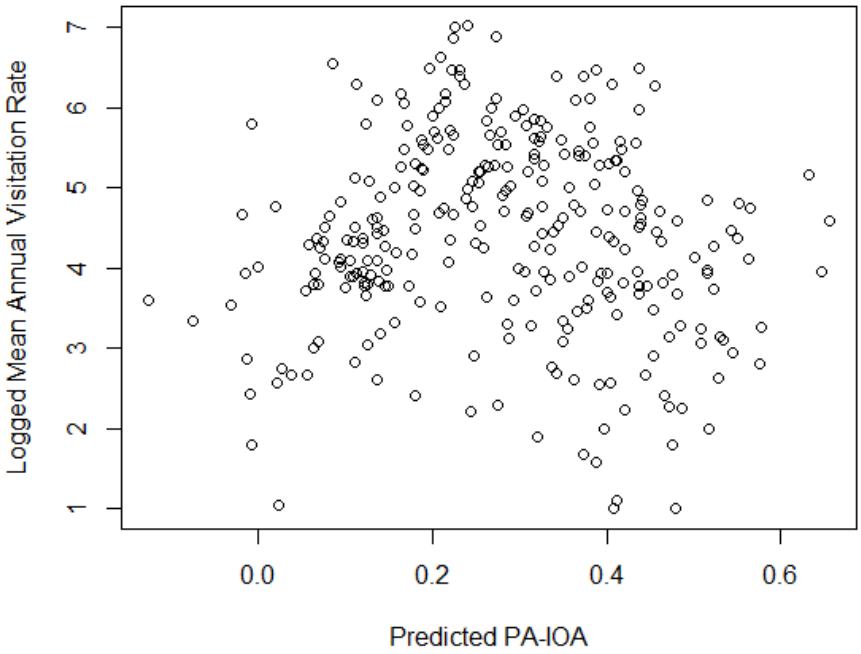


Figure 3.6: Mean annual visitation rates (logged) for protected areas, as a function of the predicted number of sources that selected each protected area (PA-IOA), from the best negative binomial GLM (n = 302).

Table 3.10 lists PAs with the highest (1) actual PA-IOA values, based on data extracted from the sources, (2) predicted PA-LOS values, derived from the best binary GLM, and (3) predicted PA-IOA values, derived from the best negative binomial GLM.

Collectively, Figures 3.7A, 3.7B and 3.7C map the global distribution of all 48,715 PAs of interest, whilst Figures 3.8A, 3.8B and 3.8C map the actual PA-IOA scores for the 536 PAs that were mentioned by at least one of the sources. PAs that received the highest actual PA-IOA values include Panatai National Park in Brazil (Figure 3.8A), Yellowstone National Park in North America (Figure 3.8A), and Serengeti National Park in Tanzania (Figure 3.8B). Figures 3.9A, 3.9B and 3.9C highlight PAs that were identified as WBT destinations by the best binary GLM i.e. PAs in Figure 3.2, quadrants A and B. Collectively, Figures 3.10A, 3.10B and 3.10C map the predicted PA-LOS values of all 48,715 PAs of interest, based on the best binary GLM's predictions. PAs that are most likely to be selected as WBT destinations are found in upper Amazonia (Figures 3.10A), sub-Saharan Africa (Figures 3.10B) and Asia (Figures 3.10C), whilst PAs in North America (Figures 3.10A), Europe (Figures 3.10B) and Australasia (Figures 3.10C) are less likely to be selected as sites for WBT, by the best binary GLM. PAs with the highest predicted PA-IOA values are found in upper Amazonia (Figure 3.11A), sub-Saharan Africa (Figure 3.11B) and Indonesia (Figure 3.11C), whilst PAs with the lowest predicted PA-IOA are found in the North America (Figure 3.11A), Europe (Figure 3.11B) and Australasia (Figure 3.11C), based on the best negative binomial GLM's predictions. Figures 3.12A, 3.12B and 3.12C highlight PAs with high PA-IOA values, based on the 1,995 false positive WBT destinations, defined as PAs in Figure 3.2, quadrant A. Highlighted PAs are largely found in upper Amazonia (Figure 3.12A) and sub-Saharan Africa (Figure 3.12B).

Table 3.10: Protected areas (PAs) with the highest (1) actual index-of-attractiveness (PA-IOA) values, (2) predicted likelihood-of-selection (PA-LOS) values, derived from the best binary GLM, and (3) predicted PA-IOA values, derived from the best negative binomial GLM. PA-IOA is defined as the number of reviewed sources that mention each PA.

Rank	PAs with highest actual PA-IOA				PAs with highest predicted PA-LOS				PAs with highest predicted PA-IOA			
	PA Name	Management Category	Continent	PA-IOA	PA Name	Management Category	Continent	PA-LOS	PA Name	Management Category	Continent	PA-IOA
1	Serengeti	National Park	Africa	159	Namib-Naukluft	National Park	Africa	1.00	Gambella	National Park	Africa	37.89
2	Pantanal Matogrossense	National Park	South America	105	Hwange	National Park	Africa	1.00	Ruaha	National Park	Africa	35.66
3	Masai Mara	National Park	Africa	96	Tsavo East	National Park	Africa	1.00	Hwange	National Park	Africa	33.96
4	Moremi	Wilderness area	Africa	96	Ruaha	National Park	Africa	1.00	Serengeti	National Park	Africa	33.57
5	Kaziranga	National Park	Asia	96	Serengeti	National Park	Africa	0.99	Tsavo East	National Park	Africa	33.19
6	Yellowstone	National Park	North America	92	Tsavo West	National Park	Africa	0.99	Kafue	National Park	Africa	33.03
7	Kanha	National Park	Asia	91	Etosha	National Park	Africa	0.99	Mago	National Park	Africa	33.01
8	Etosha	National Park	Africa	91	Skeleton Coast Park	National Park	Africa	0.99	Chobe	Wilderness area	Africa	32.33
9	Chitwan	National Park	Asia	79	Gambella	National Park	Africa	0.99	Jaú	National Park	South America	31.48
10	Chobe	Wilderness area	Africa	75	Murchison Falls	National Park	Africa	0.99	Tsavo West	National Park	Africa	30.57

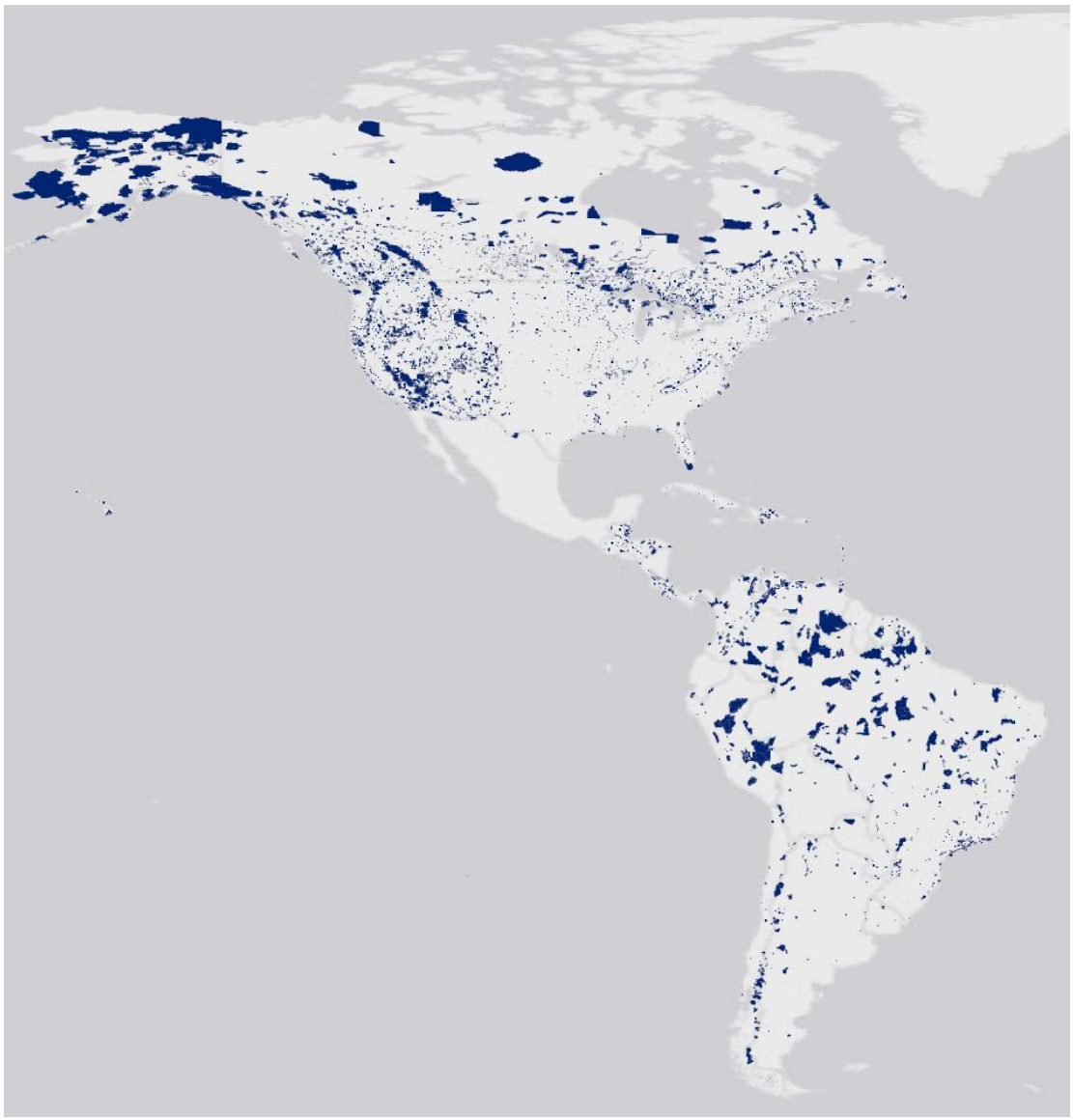


Figure 3.7A: Distribution of North American and South American protected areas, for which data were available (n=16,322).

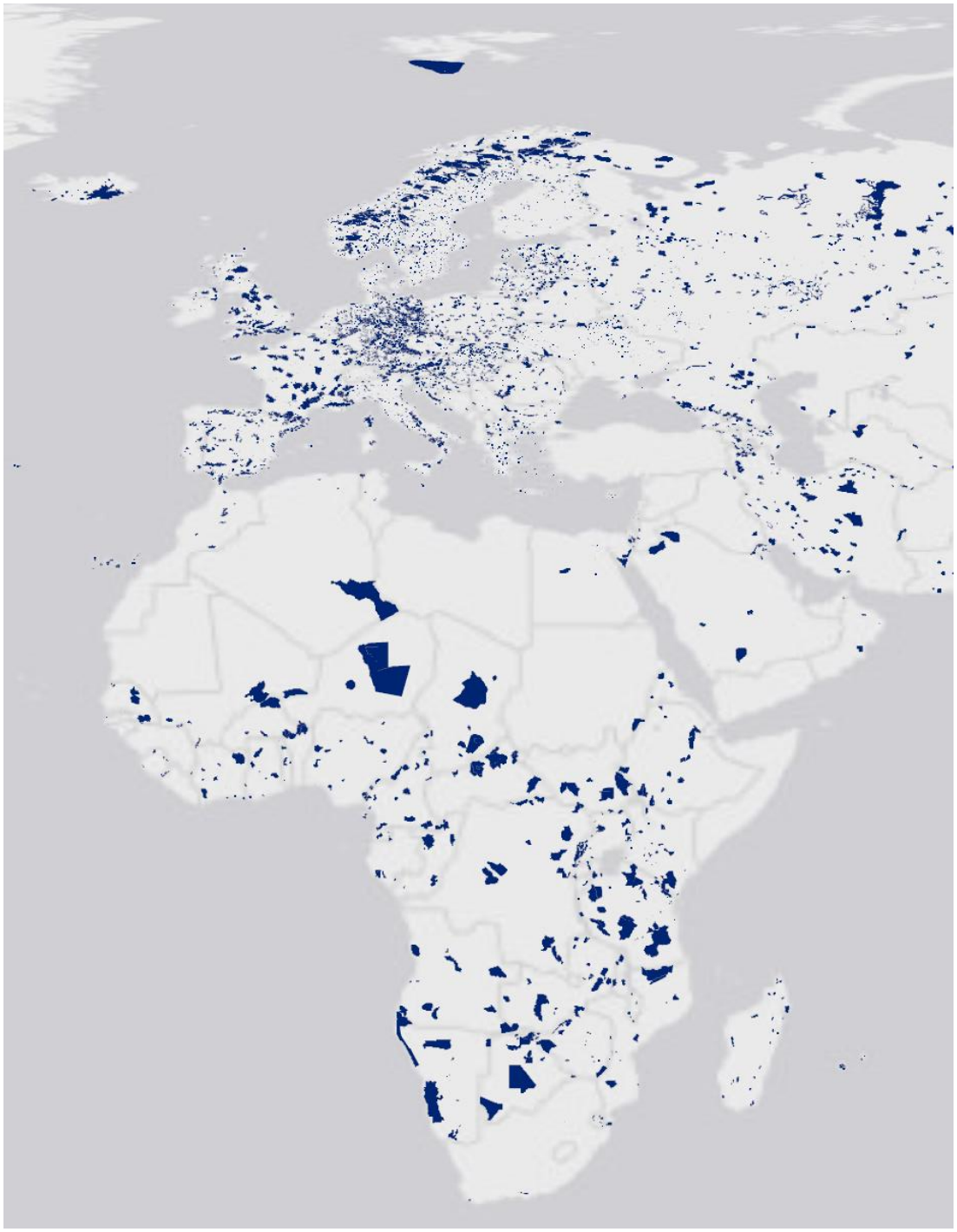


Figure 3.7B: Distribution of African and European protected areas, for which data were available (n=19,829).

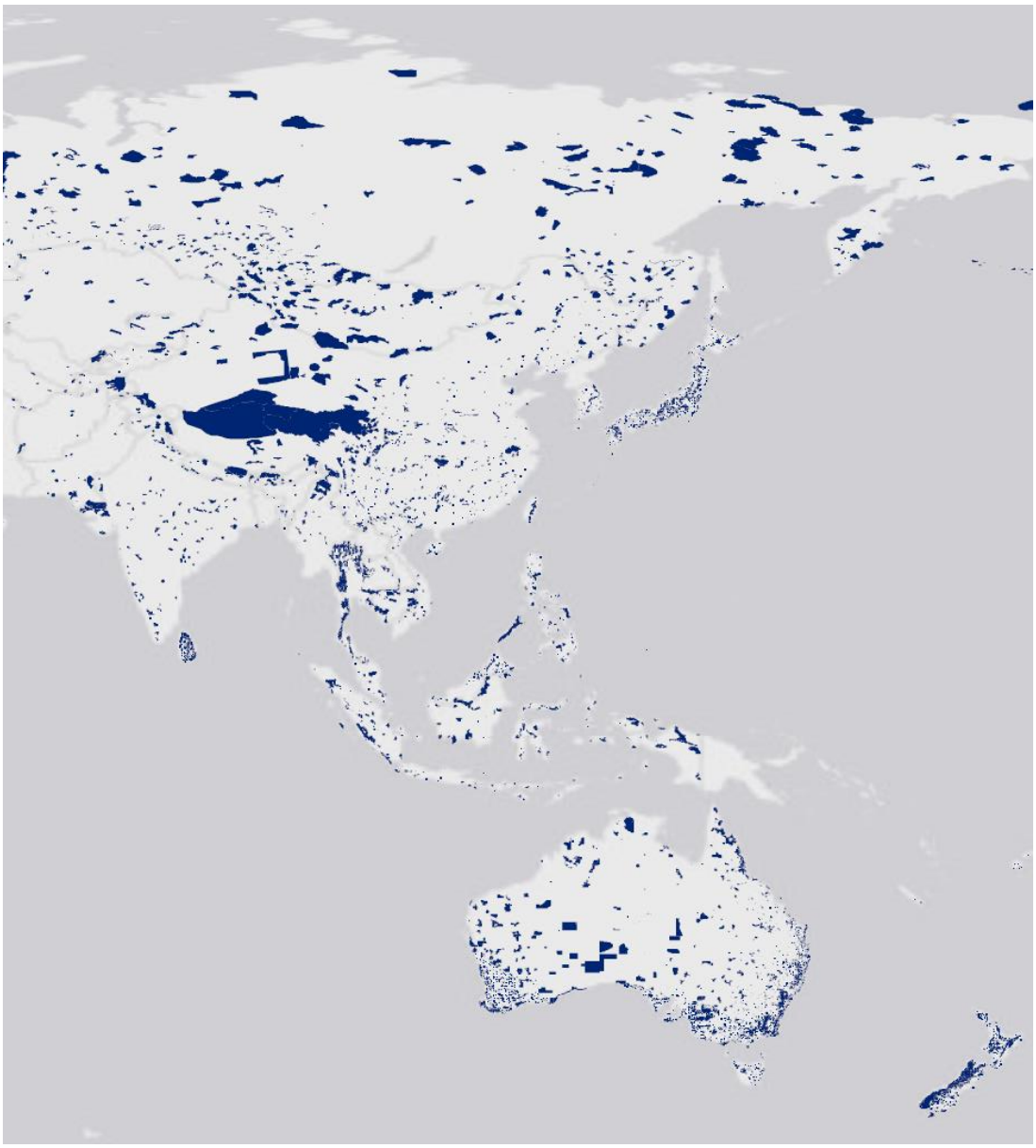


Figure 3.7C: Distribution of Asian and Australasian protected areas, for which data were available (n=12,252).

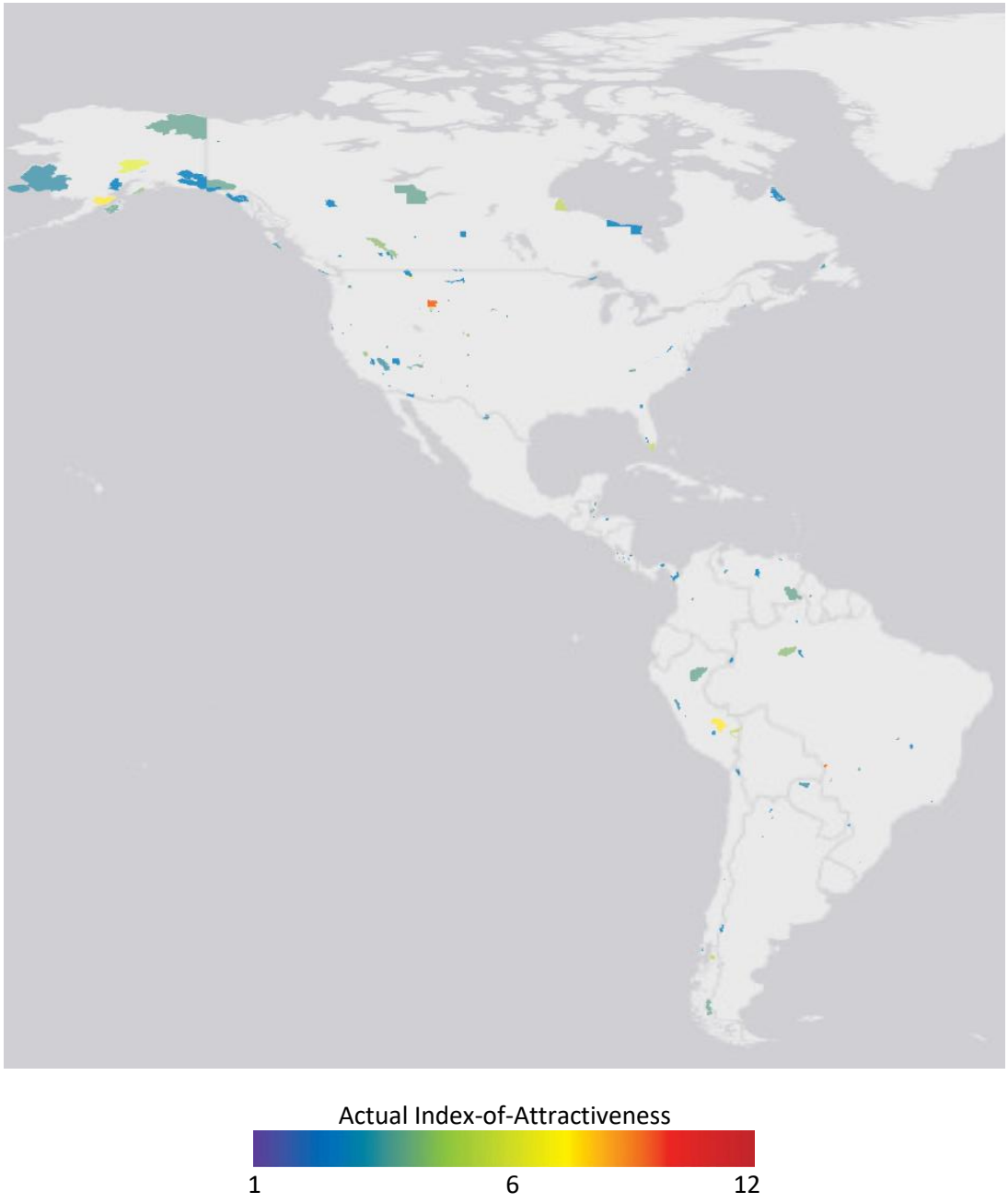


Figure 3.8A: Protected area index-of-attractive (PA-IOA) values for all North American and South American protected areas that were mentioned by at least one of the sources. PA-IOA is defined as the number of reviewed sources that mention each protected area (n = 149).

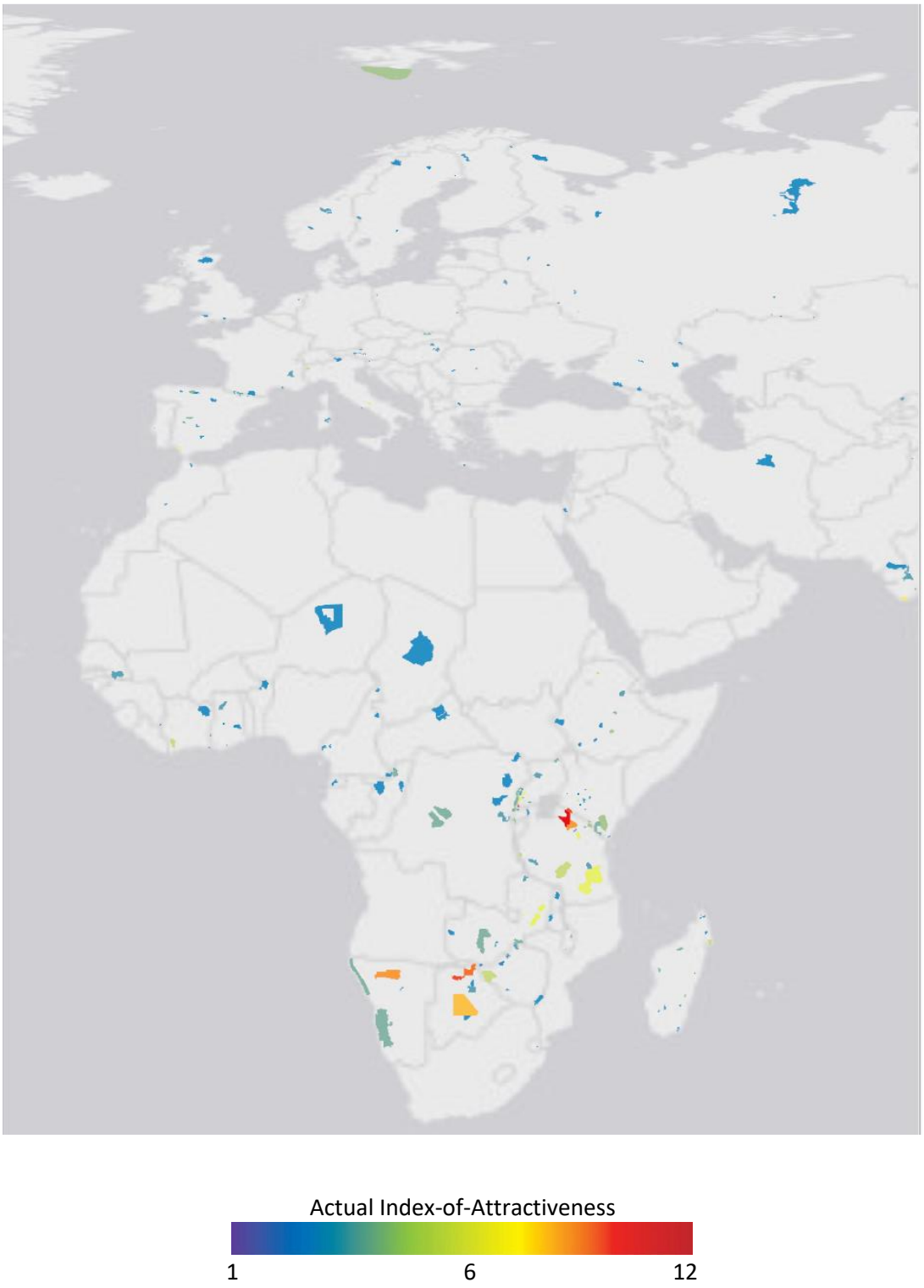


Figure 3.8B: Protected area index-of-attractive (PA-IOA) values for all African and European protected areas that were mentioned by at least one of the sources. IOA is defined as the number of reviewed sources that mention each protected area (n = 212).

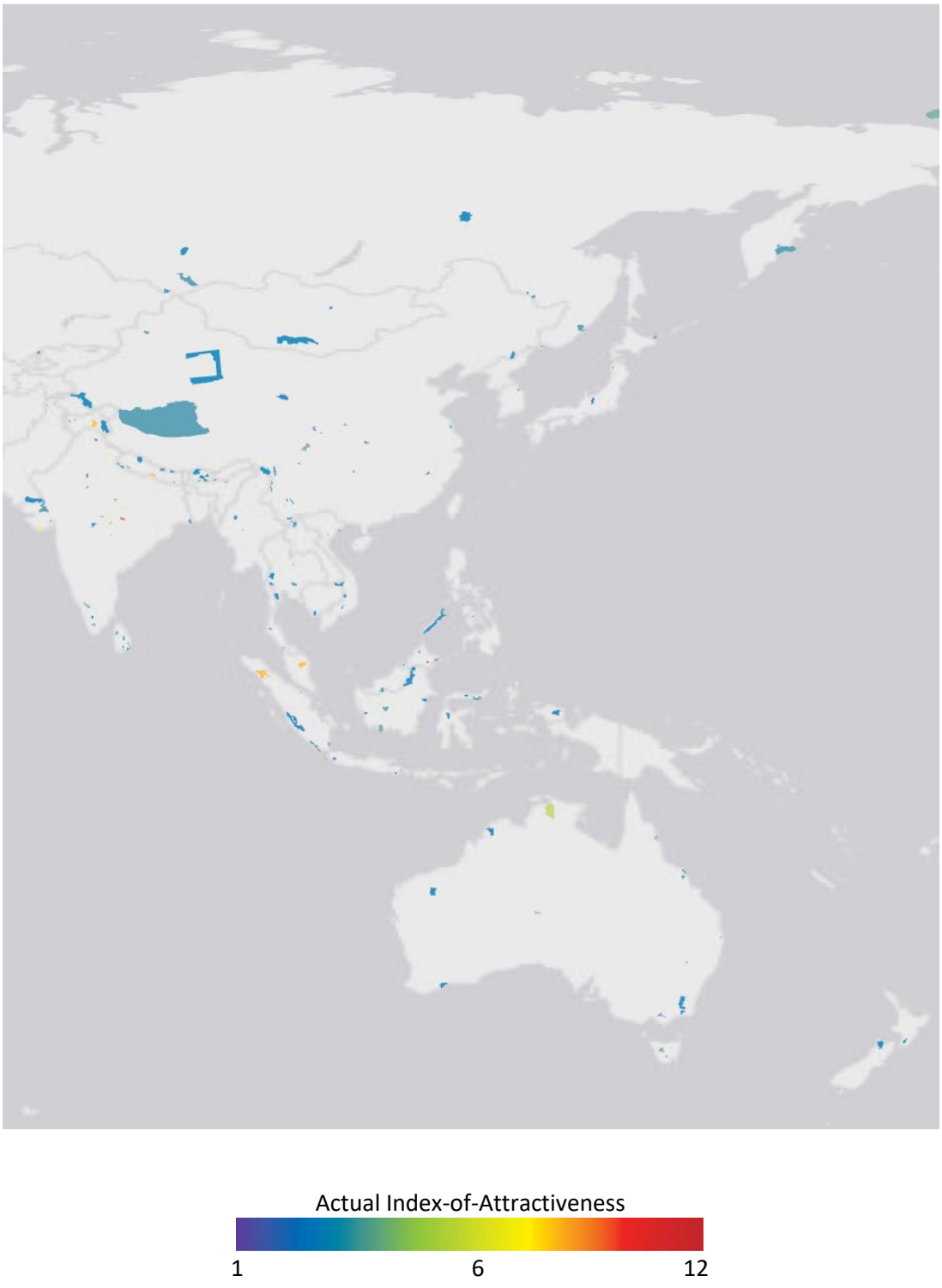


Figure 3.8C: Protected area index-of-attractive (PA-IOA) values for all Asian and Australian protected areas that were mentioned by at least one of the sources. IOA is defined as the number of reviewed sources that mention each protected area (n = 268).

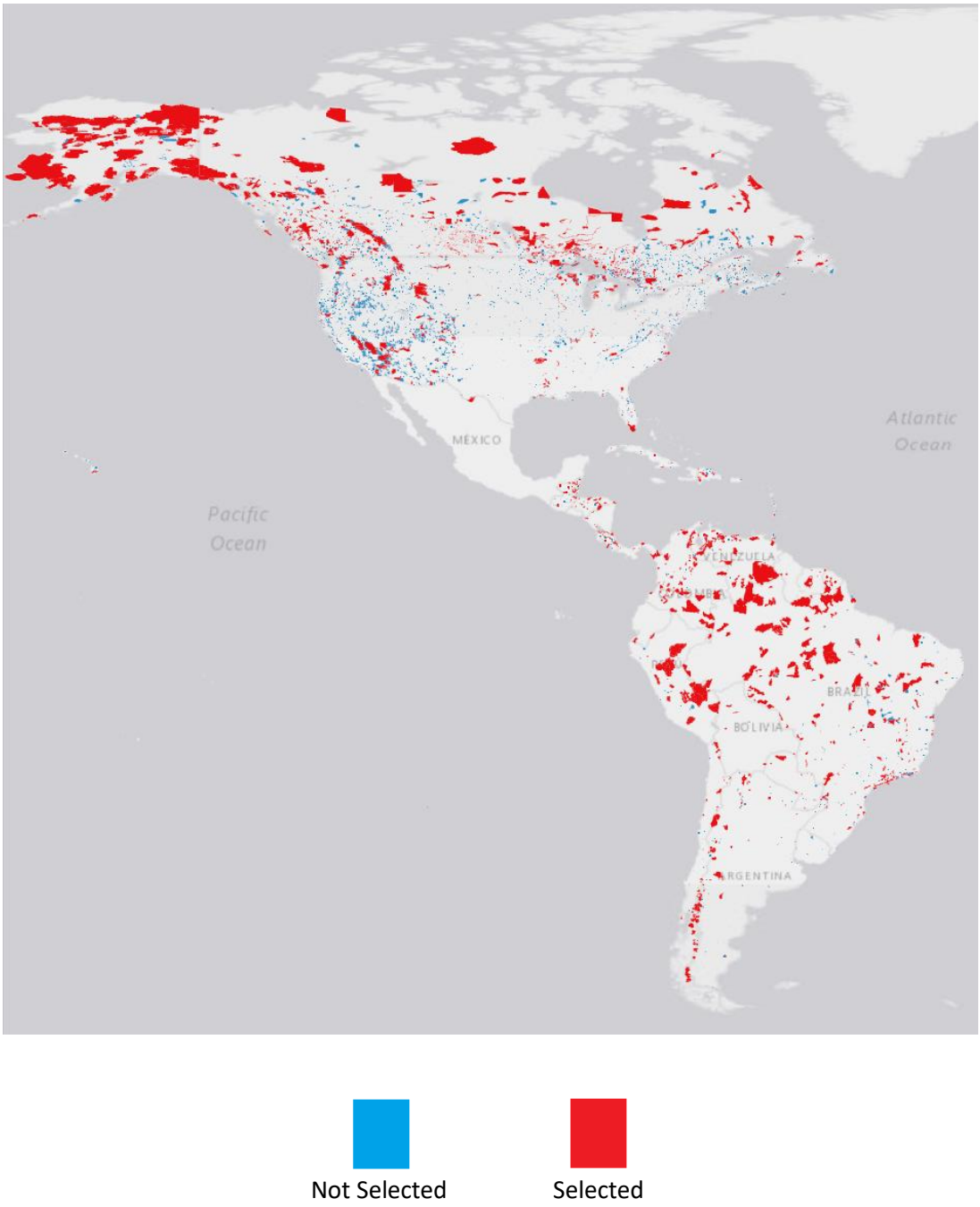


Figure 3.9A: North American and South American protected areas that were selected (red) and not selected (blue) as wildlife-based tourism destinations by the best binary GLM (n=16,322).

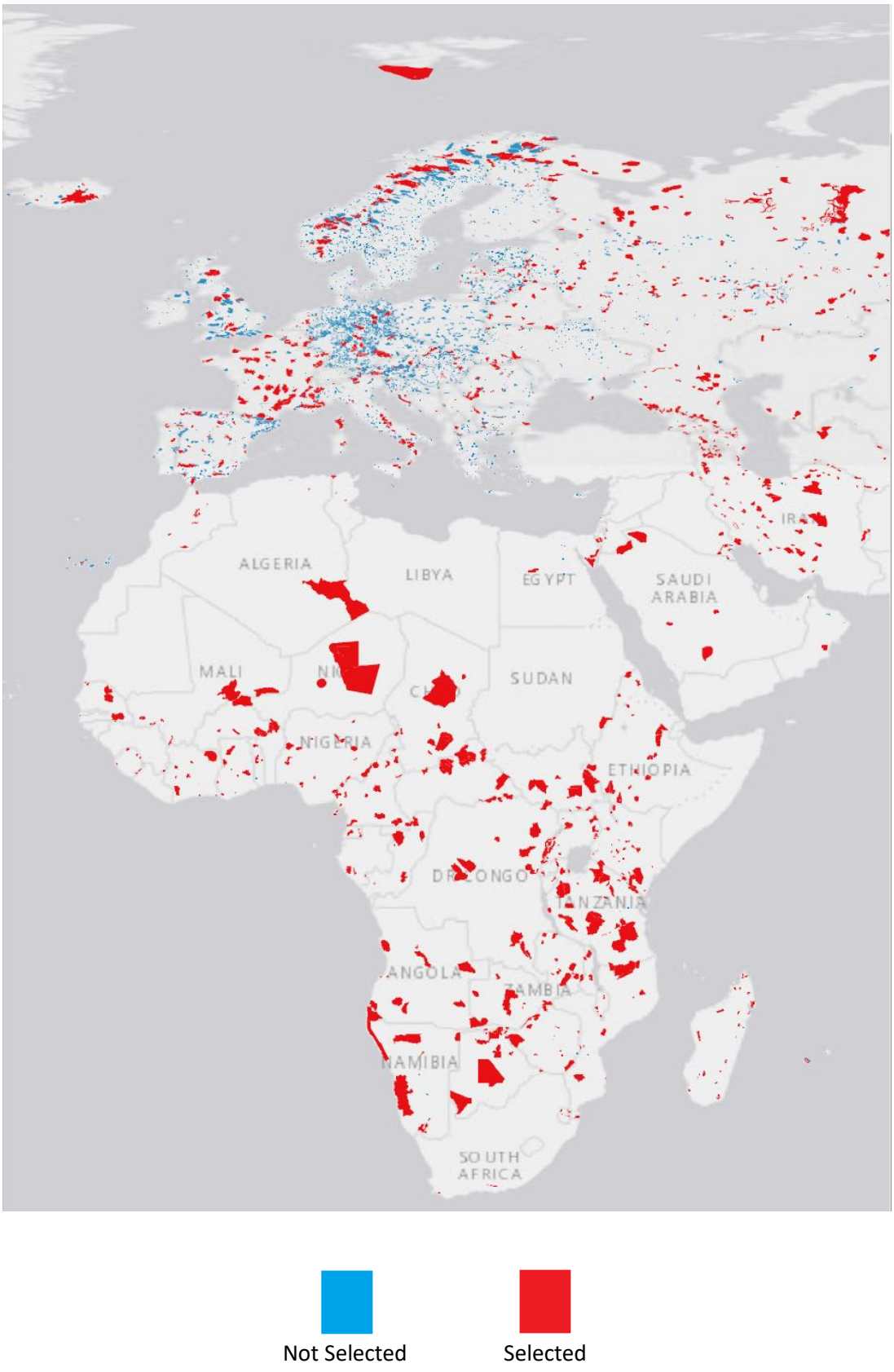


Figure 3.9B: African and European protected areas that were selected (red) and not selected (blue) as wildlife-based tourism destinations by the best binary GLM (n=19,829).

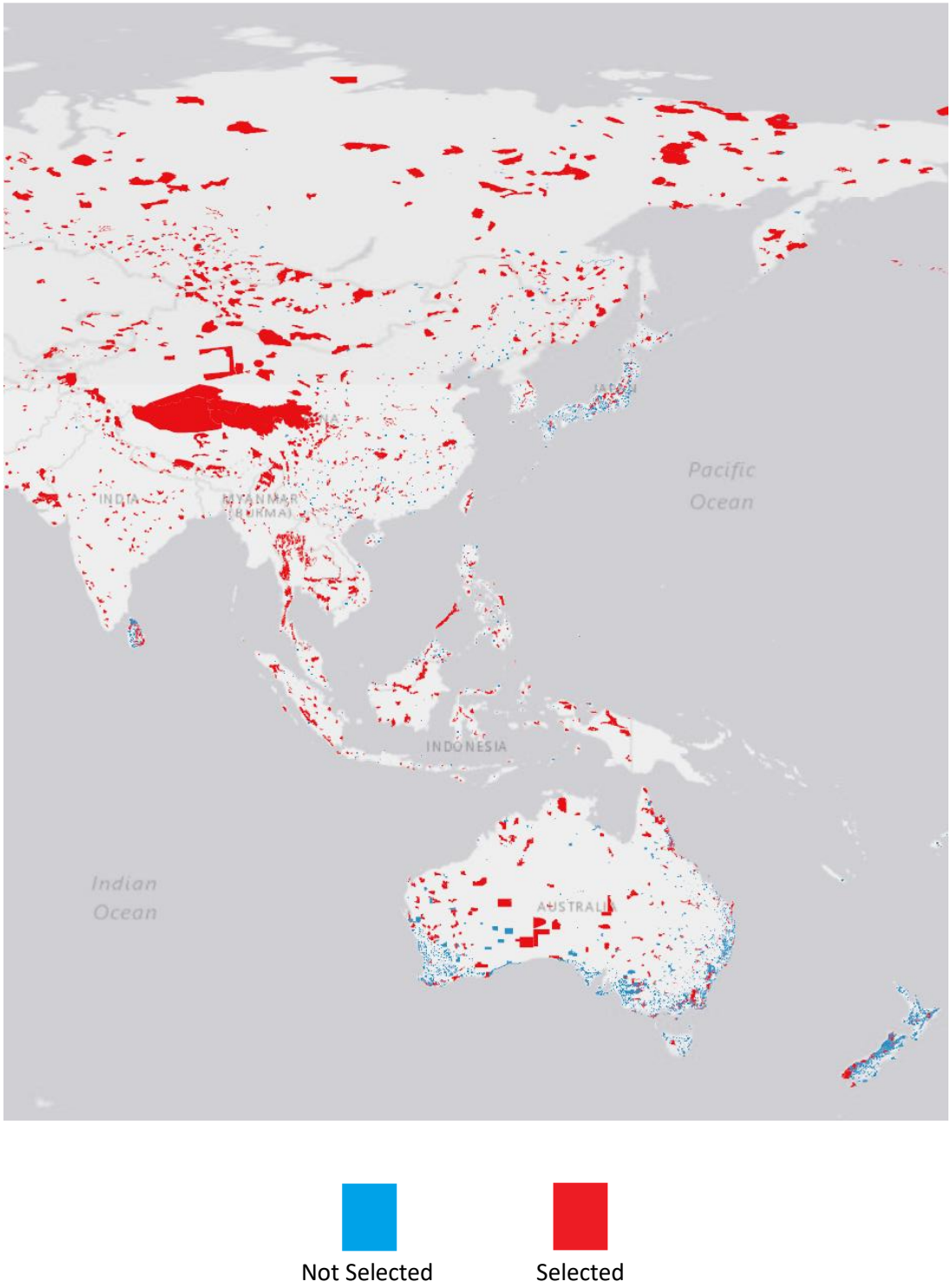


Figure 3.9C: Asian and Australasian protected areas that were selected (red) and not selected (blue) as wildlife-based tourism destinations by the best binary GLM (n=12,252).

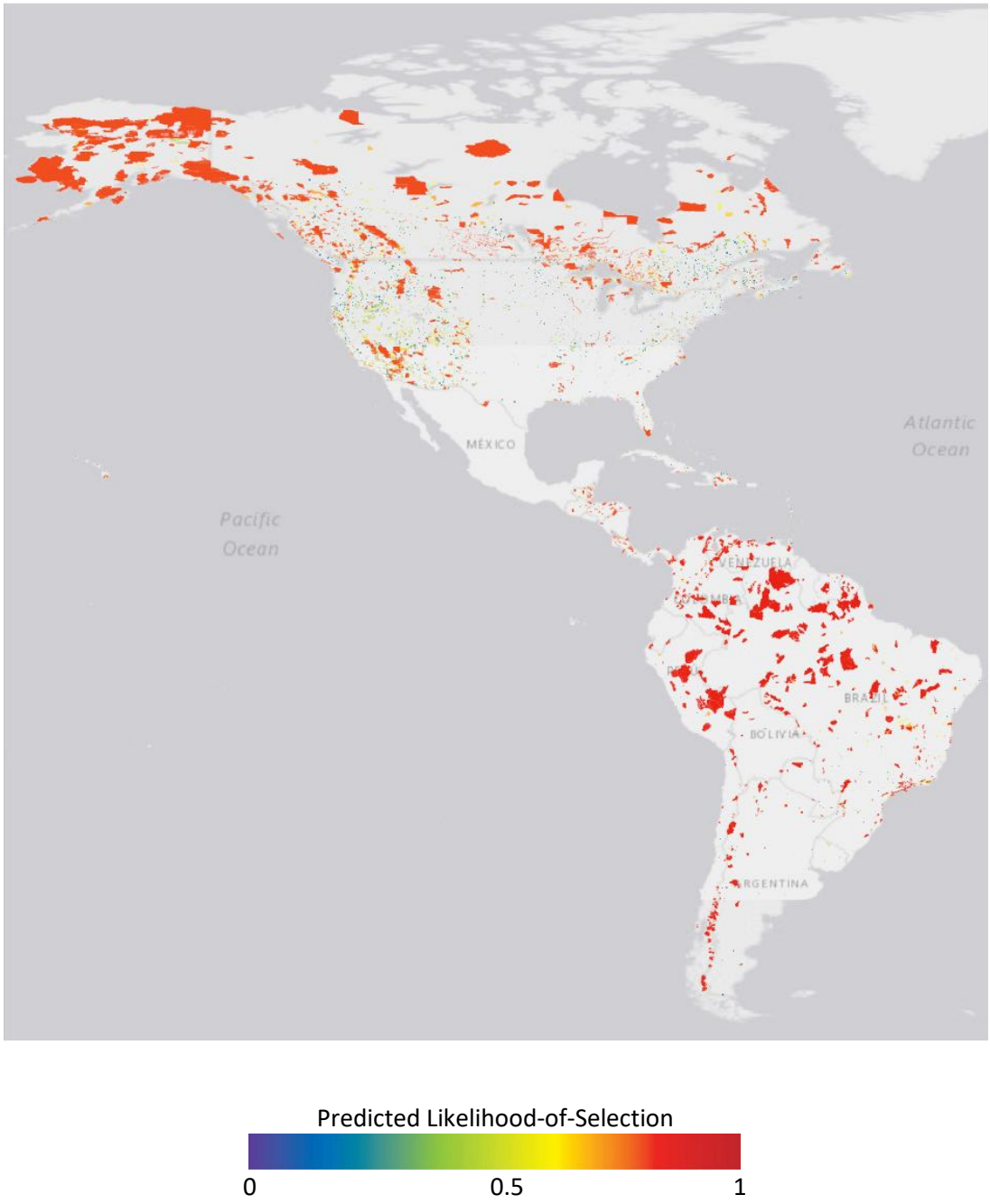


Figure 3.10A: Predicted protected area likelihood-of-selection (PA-LOS) values for all North American and South American protected areas (for which data were available). PA-LOS is defined as the likelihood that a protected area will be selected as a wildlife-based tourism destination, by the best binary GLM (n=16,322).

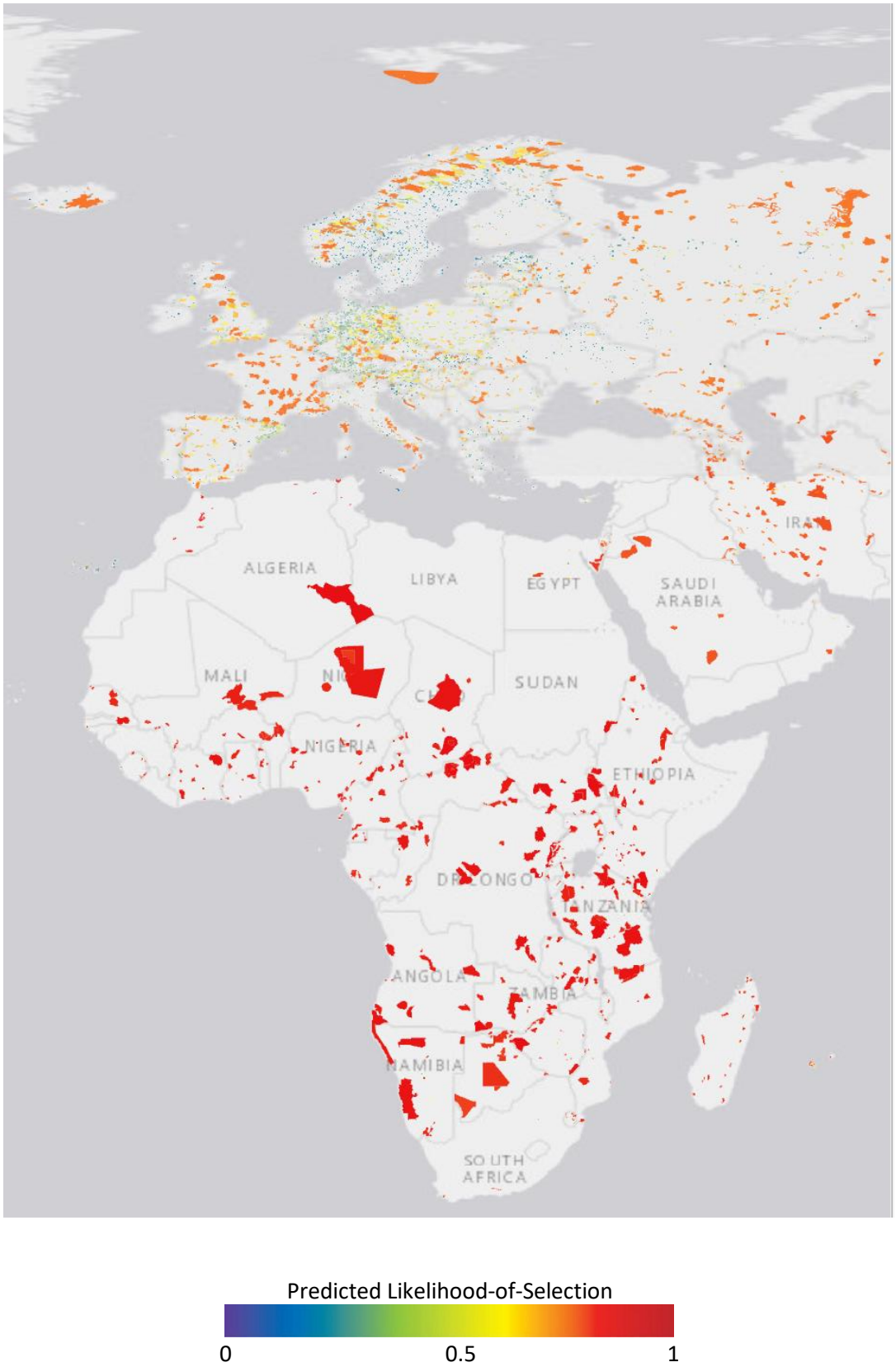


Figure 3.10B: Predicted protected area likelihood-of-selection (PA-LOS) values for all African and European protected areas (for which data were available). PA-LOS is defined as the likelihood that a protected area will be selected as a wildlife-based tourism destination, by the best binary GLM (n=19,829).

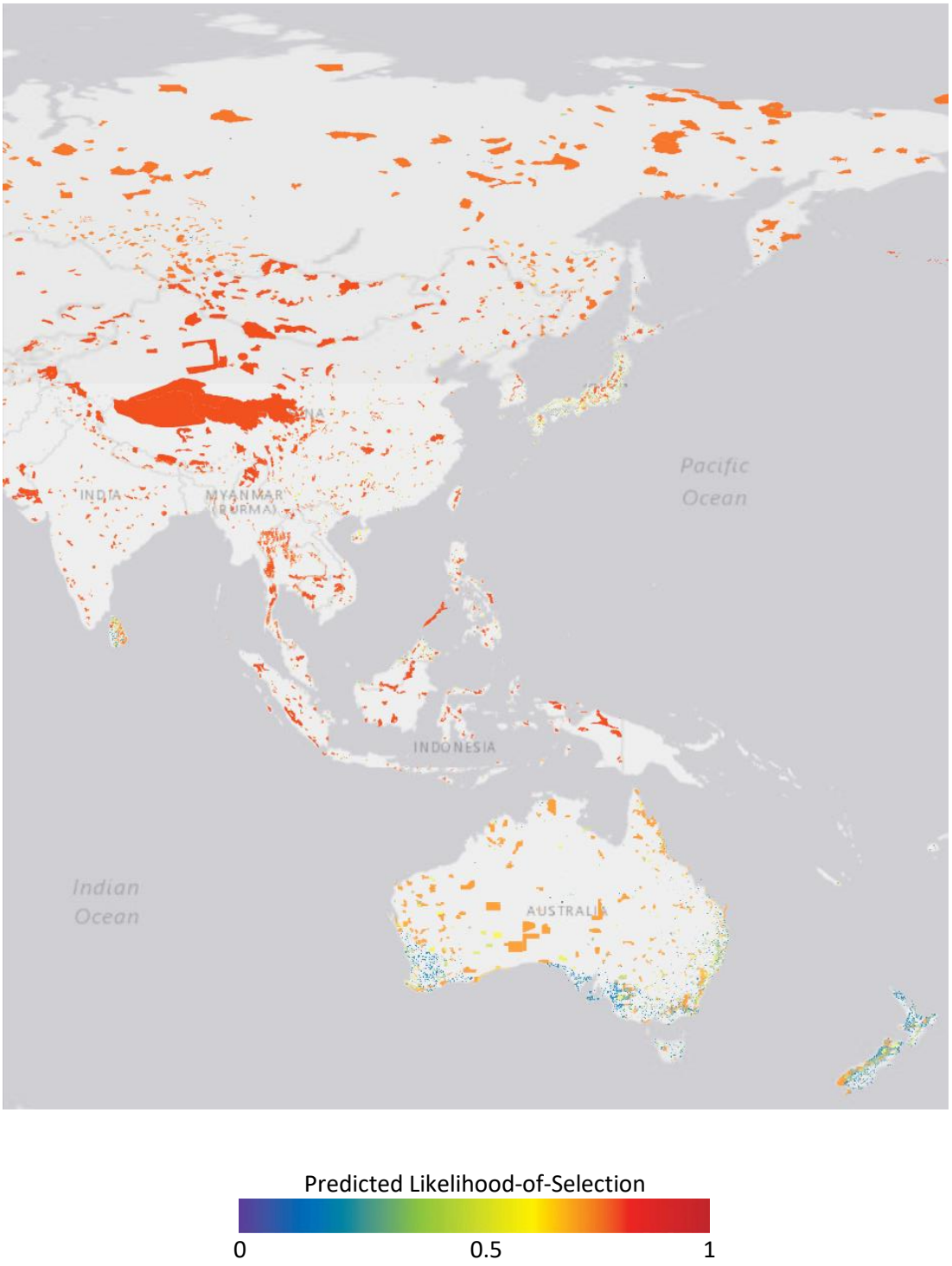


Figure 3.10C: Predicted protected area likelihood-of-selection (PA-LOS) values for all Asian and Australasian protected areas (for which data were available). PA-LOS is defined as the likelihood that a protected area will be selected as a wildlife-based tourism destination, by the best binary GLM (n=12,252).

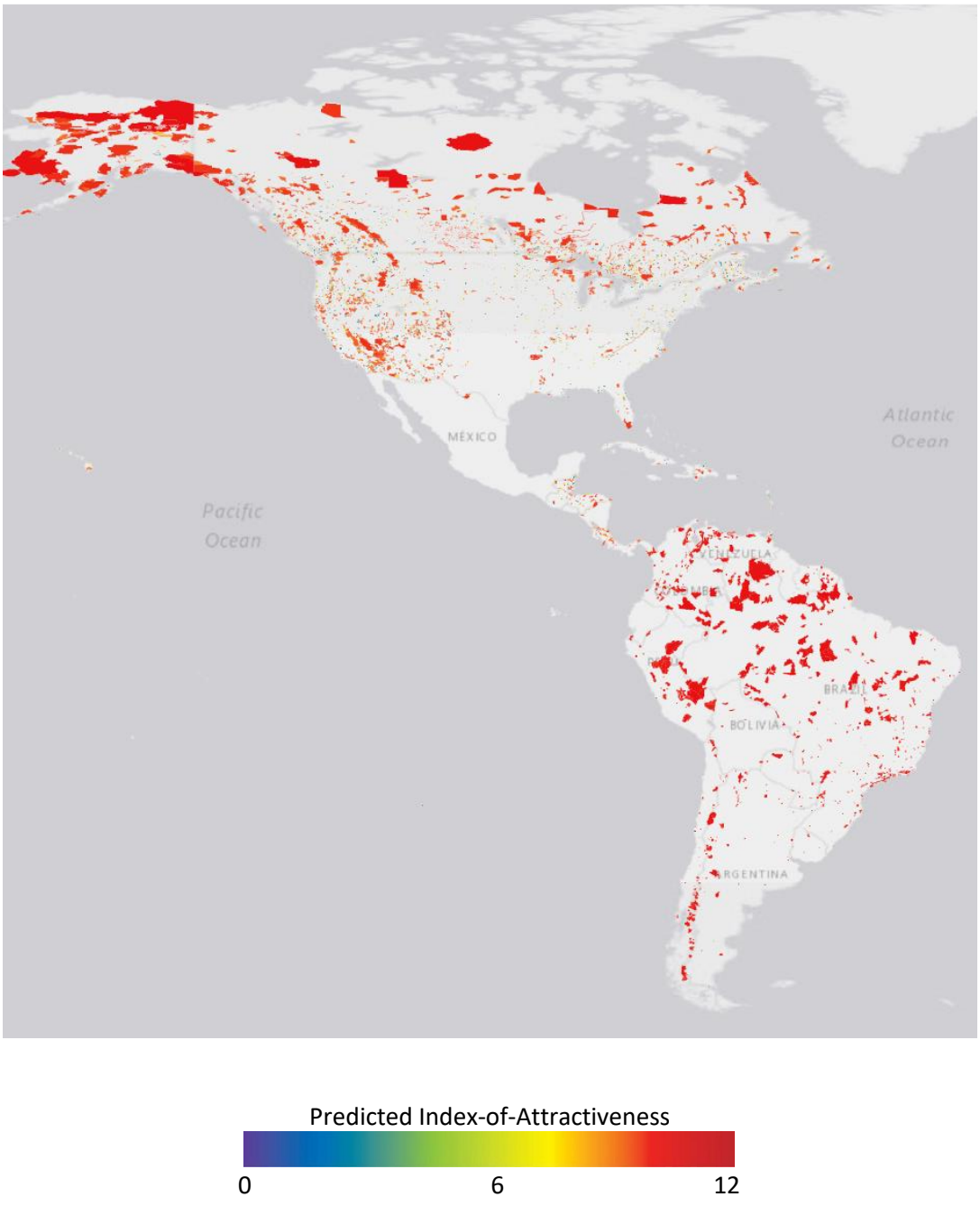


Figure 3.11A: Predicted protected area index-of-attractiveness (PA-IOA) values for all North American and South American protected areas (for which data were available). Predicted PA-IOA is defined as the predicted number of reviewed sources that mentioned each protected area, based on the best negative binomial GLM's predictions (n=16,322).

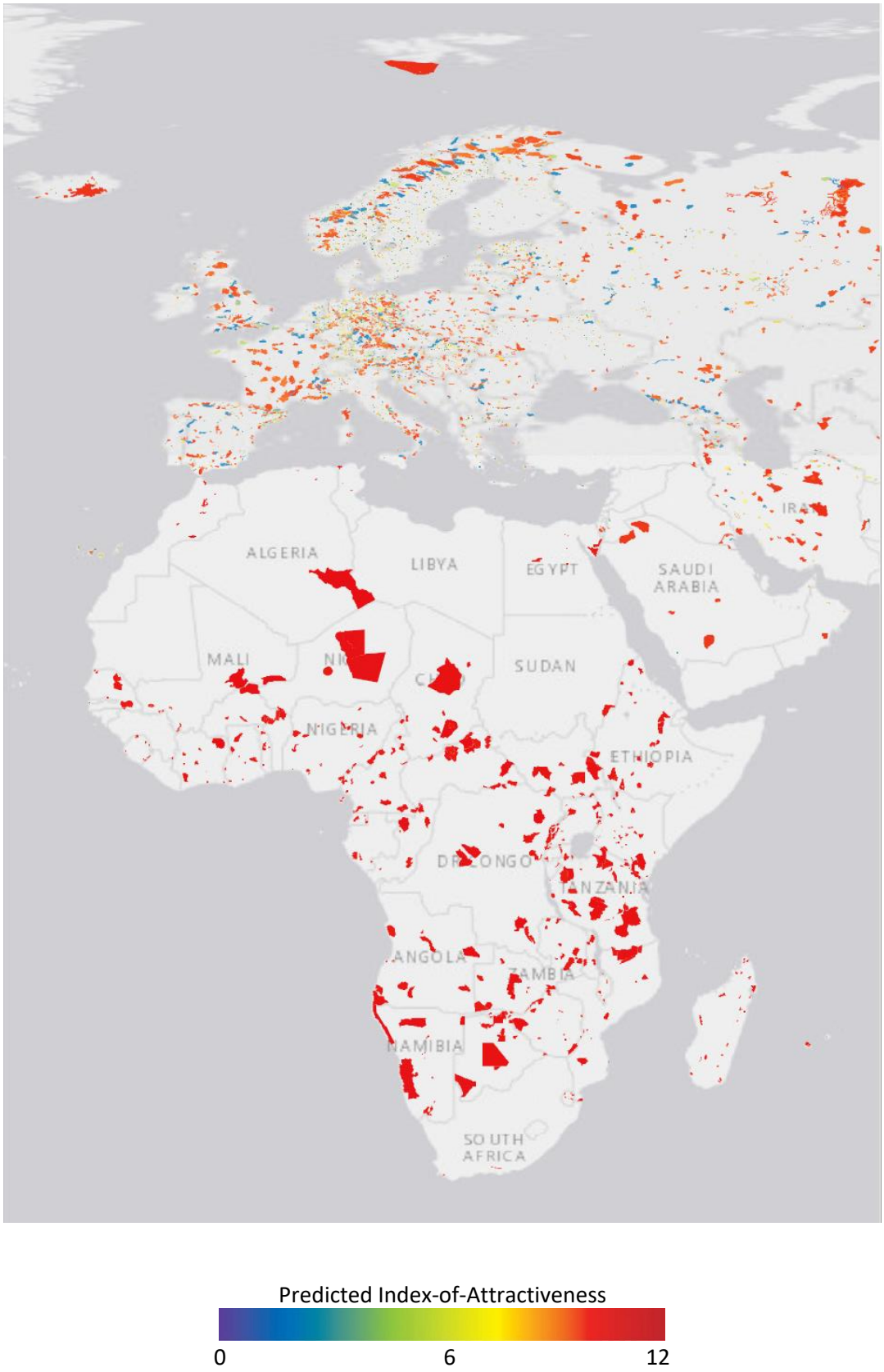


Figure 3.11B: Predicted protected area index-of-attractiveness (PA-IOA) values for all African and European protected areas (for which data were available). Predicted PA-IOA is defined as the predicted number of reviewed sources that mentioned each protected area, based on the best negative binomial GLM's predictions (n=19,829).

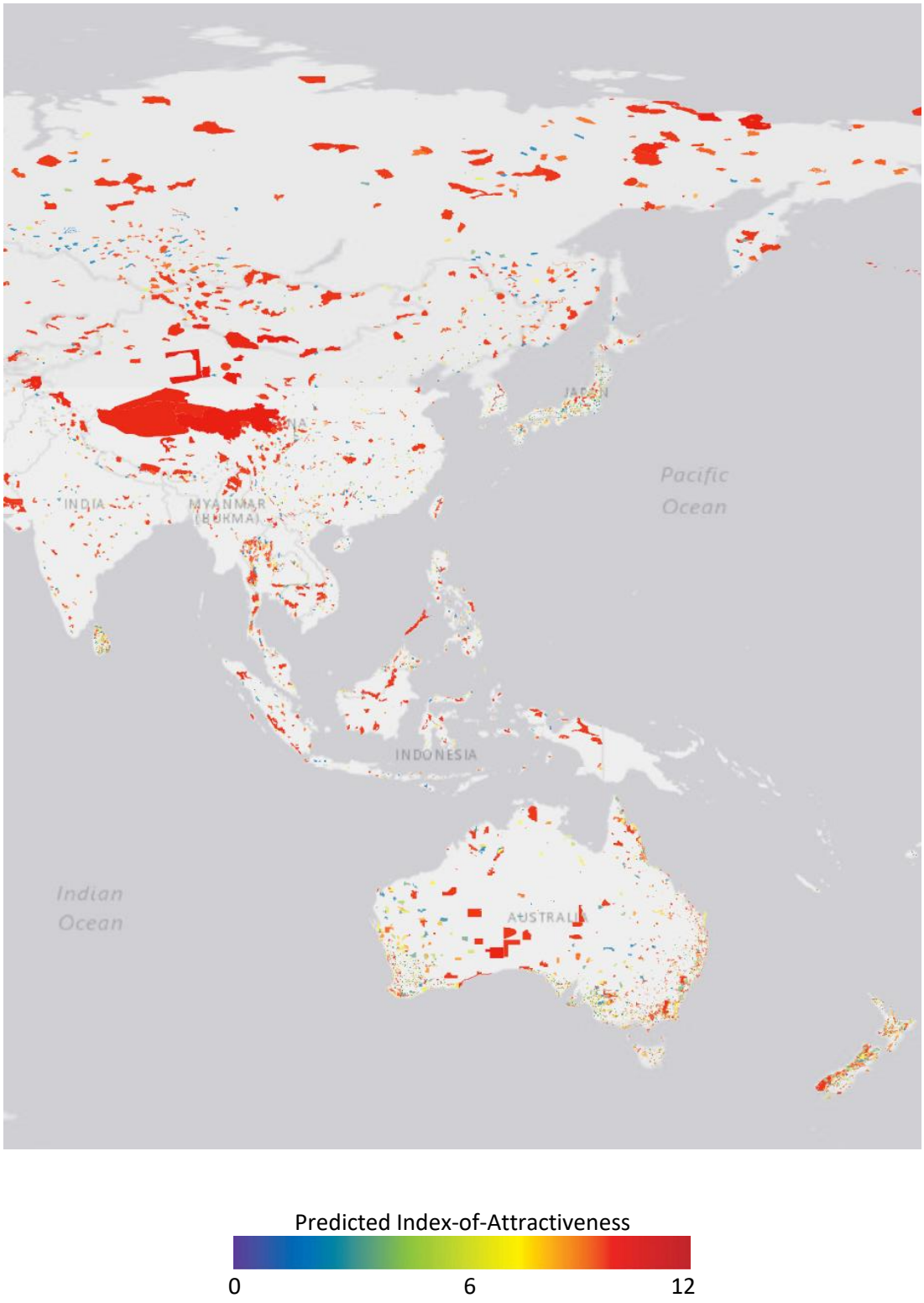


Figure 3.11C: Predicted protected area index-of-attractiveness (PA-IOA) values for all Asia and Australasian protected areas (for which data were available). Predicted PA-IOA is defined as the number of reviewed sources that mentioned each protected area, based on the best negative binomial GLM's predictions (n=12,252).

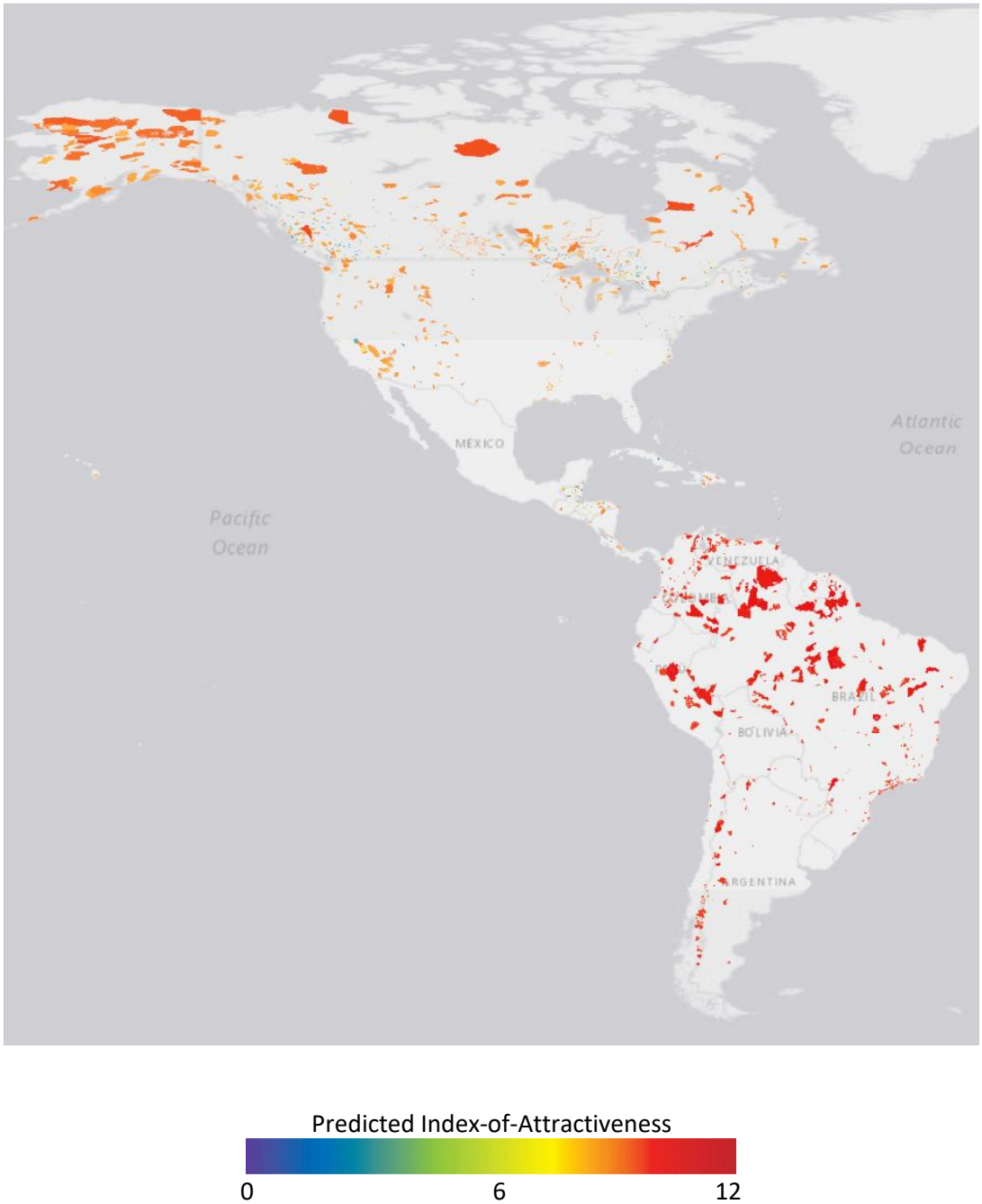


Figure 3.12A: Predicted protected area index-of-attractiveness (PA-IOA) values for all North American and South American 'false positive wildlife-based tourism destinations', defined as protected areas in Figure 3.2, quadrant A. Predicted PA-IOA is defined as the predicted number of reviewed sources that mentioned each protected area, based on the best negative binomial GLM's predictions (n=1,181).

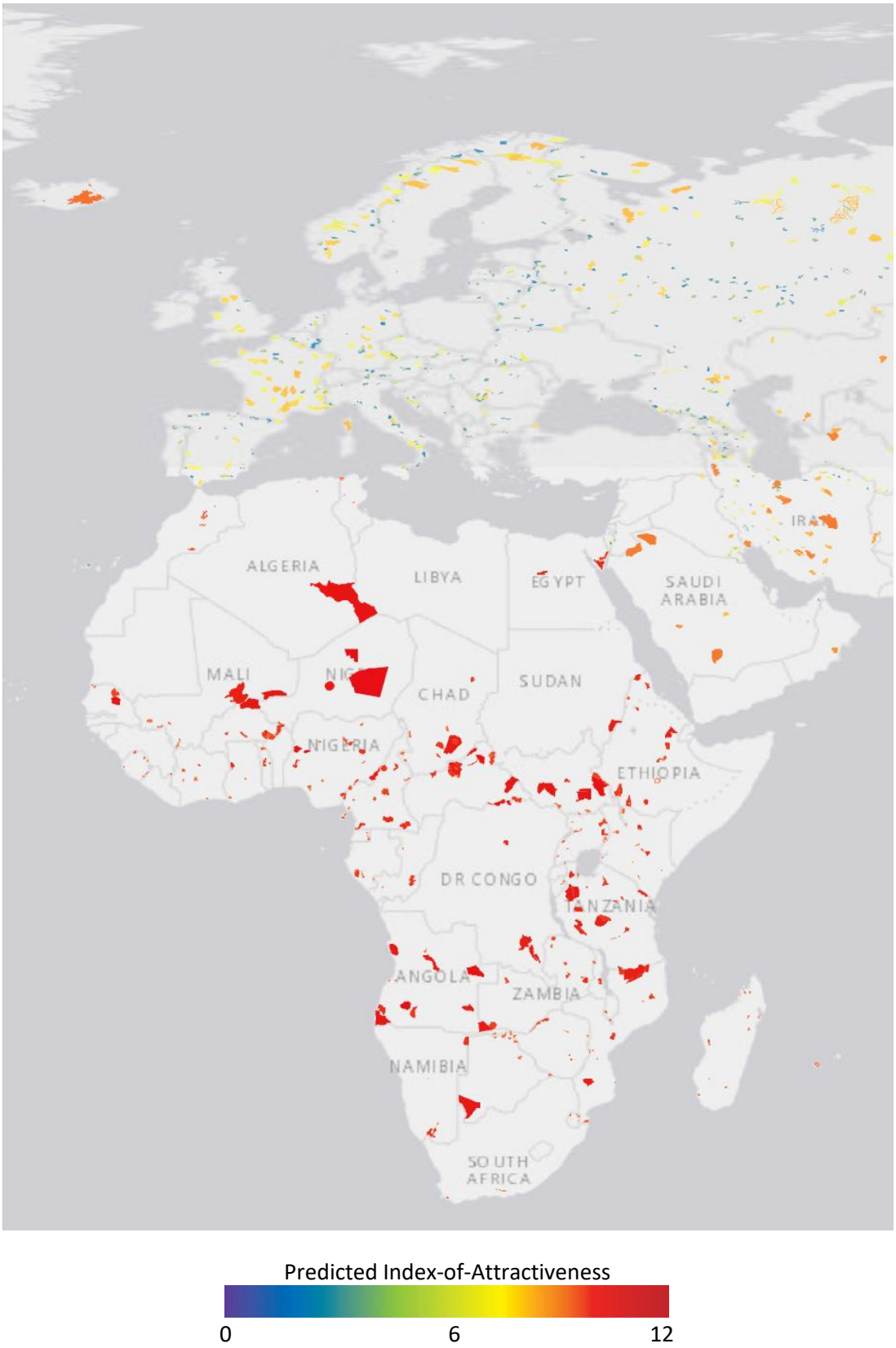


Figure 3.12B: Predicted protected area index-of-attractiveness (IOA) values for all European and African 'false positive wildlife-based tourism destinations', defined as protected areas in Figure 3.2, quadrant A. Predicted PA-IOA is defined as the predicted number of reviewed sources that mentioned each protected area, based on the best negative binomial GLM's predictions (n=1,000).

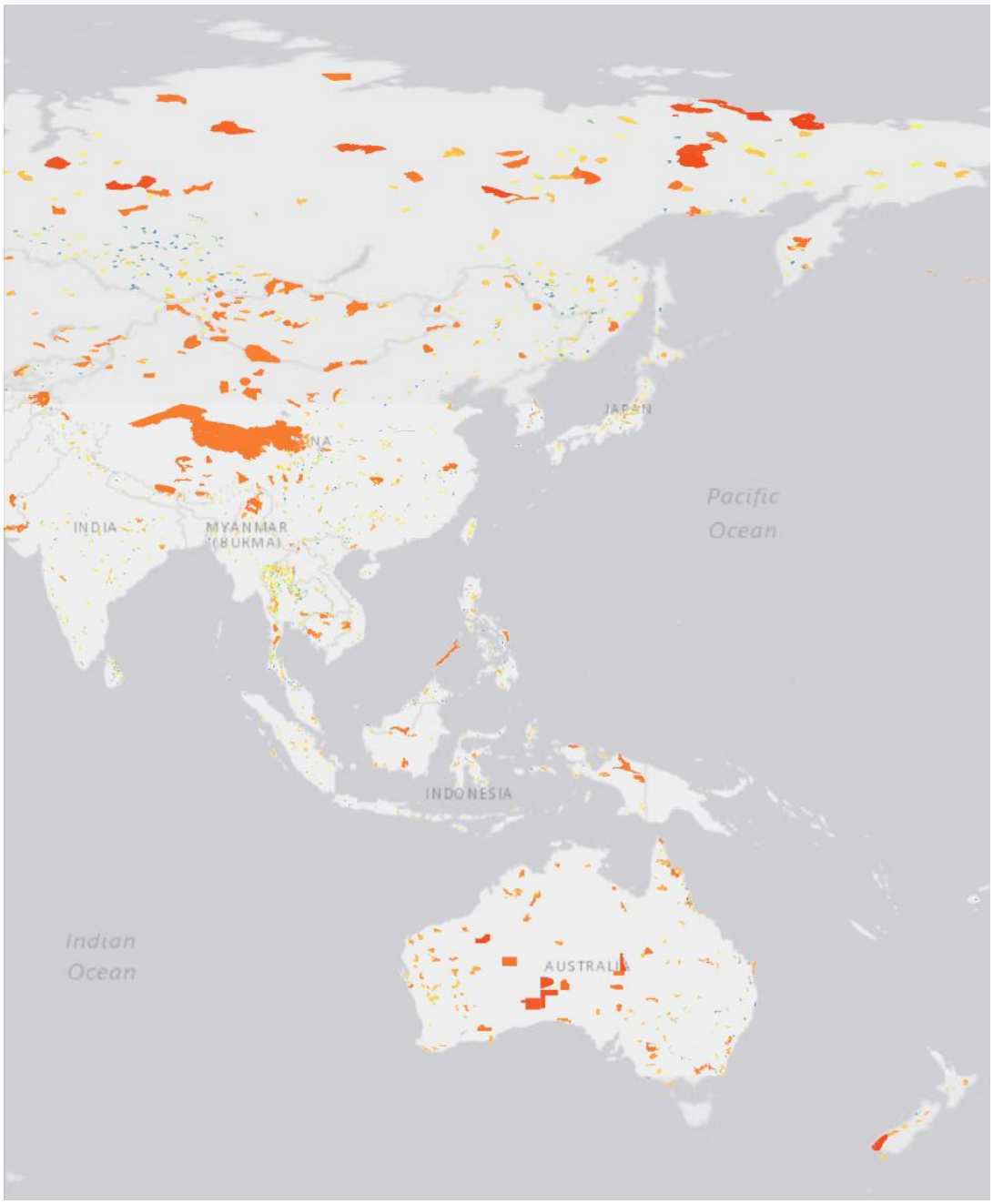


Figure 3.12C: Predicted protected area index-of-attractiveness (PA-IOA) values for all Asian and Australasian 'false positive wildlife-based tourism destinations', defined as protected areas in Figure 3.2, quadrant A. Predicted PA-IOA is defined as the predicted number of reviewed sources that mentioned each protected area, based on the best negative binomial GLM's predictions (n=1,287).

3.4 DISCUSSION

3.4.1 Size, Accessibility and Wildlife Attractiveness

The results from this study confirm the importance of PA size, accessibility and wildlife attractiveness as key features of PAs that make them attractive to WB-tourists (Hanink & Stutts 2002; Deng *et al.* 2002; Akama & Kieti 2003; Higginbottom & Buckley 2003; Lindsey *et al.* 2007; Neuvonen *et al*. 2010; Balmford *et al*. 2015). Both the binary GLM (for PA-LOS) and negative binomial GLM (for PA-IOA) predict larger, less remote PAs, with higher wildlife attractiveness values, such as Serengeti National Park in Tanzania, are more attractive to WB-tourists than smaller, more remote PAs, with lower wildlife attractiveness values (Table 3.10). This suggests that future loss of TM species (specifically large, threatened TM species) from a PA may reduce the area's potential as a WBT destination. Greater investment in TM species conservation is therefore required to help stem the loss of these species (Barnosky *et al.* 2011; Ceballos *et al.* 2015). This finding also suggests that larger areas should be protected, closer to international airports, to increase their attractiveness as WBT destinations to WB-tourists.

Protecting larger areas could have positive implications for conservation as the number and rate of species extinctions in PAs declines with increases in PA size (Brashares *et al.* 2001; Newmark 1987; Rivard *et al.* 2000; Friedlander *et al.* 2007; Gurd *et al*. 2001). Larger PAs are usually more able to maintain viable populations of species than smaller PAs, particularly of those species that occur at low densities (Brashares 2003; Curran *et al*. 2004; Gurd *et al*. 2001; Laidlaw 2000; Woodroffe & Ginsberg 1998). Protecting larger areas also allows for different management plans to be implemented, for species with conflicting management requirements, in different regions of the same PA; opportunities to do so in smaller PAs are limited (Beaudry *et*

al. 2016). However, protecting larger areas is only effective when sufficient funding is available, which is rare, highlighting the need for all possible sources of revenue for conservation to be legalised and utilised (Gaston *et al.* 2006).

The effectiveness of PAs in conserving overall biodiversity is influenced by PA size, as well as by PA shape, proximity to other PAs and fragmentation (Williams *et al*. 2005; Lasky & Keitt 2013). Less compact (non-circular) PAs capture a greater range of environmental variation and are more likely to support viable populations, however, less compact PAs negatively influence species survival by increasing edge effects (Hansen & DeFries 2007). Short distances between PAs promote species dispersal and recolonisation of areas in which species have become locally extinct, which increases species representation and survival within individual PAs (Kitzes & Merenlender 2013). Fragmentation leads to a reduction in biodiversity representation as only more tolerant species can persist in a modified and degraded habitat (Fahrig 2003; Lasky & Keitt 2013). Future studies should consider how spatial features of PAs might affect WBT in the region and highlight areas for protection where the urgency for conservation action is greatest, for example, regions with high genetic and phylogenetic diversity, and ecological and evolutionary processes, rather than just those regions with high IOA (Myers *et al.* 2000; Cowling & Pressy 2001).

The size and location of PAs are typically determined by the distribution of people and potential land values (Knight & Crowling 2007). PAs are usually designated on low quality, infertile land that is unsuitable or too remote for human, non-conservation uses, such as agriculture, logging or urban development, rather than on the most desirable land for WBT (Chape 2004; Hoekstra *et al*. 2005). Consequently, aiming to establish large PAs closer to international airports, where land is of greater value, human population densities are higher and space is more limited, may be unrealistic. Instead, WBT operations should focus on improving the accessibility of more remote

PAs, for example by developing new and improved road networks between international airports and PAs.

Well-developed transport infrastructure is one of the most basic requirements for a WBT destination (Higginbottom & Tribe 2005). Yet, in Kenya, for example, like in many other developing countries, the state of road infrastructure is in a state of disrepair (Akama & Kieti 2003). Cracks and 'potholes' in the tarmac increase travel times, road traffic accidents and cause damage to vehicles, which can increase the maintenance and repair costs for WBT operators (Akama & Kieti 2003). Greater investment in transport infrastructure could help reduce these costs, and benefit rural communities, by improving their access to, and communication with, outside markets (Lui *et al.* 2012). However, improving the accessibility of under-utilised PAs might also increase wildlife threats, for example, from poachers. To help reconcile this with increased WBT, tour operators should help fund more intense patrols, ambushes and spot checks of PAs and provide free environmental education classes for schools and local community groups (UWA 2017).

3.4.2 Management Category and Continent

Management category and continent were identified as additional factors responsible for explaining variation in the likelihood of being selected as a WBT destination (PA-LOS). The binary model predicts that PAs in Australasia, Europe and North America are significantly less likely to be selected as WBT destinations than PAs in Africa, and that PAs in management category II (National Parks) are significantly more likely to be selected as WBT destinations than PAs in other management categories (Table 3.7). This is in accordance with previous studies that suggest designation as a National Park supports the growth of visitors to PAs (Fredman *et al*. 2007).

Large National Parks in North America, for example Yellowstone National Park and Grand Canyon National Park (Table 3.10), received high predicted PA-LOS (Figure 3.10A) and PA-IOA (Figure 3.11A) values. However, the majority of PAs in North America are relatively small, with low wildlife attractiveness values, in management categories Ia, Ib, and III (strict Nature Reserves, Wilderness Areas and Natural Monuments or Features, respectively), and received low predicted PA-LOS (Figure 3.10A) and PA-IOA (Figure 3.11A) values. In South Africa, fences are being dropped between private game parks and the Greater St Lucia Wetlands Park so that a new larger area can be jointly managed (Valentine & Bertiles 2008). The WBT potential of smaller North American PAs could be increased using a similar technique i.e. by merging local clusters together to form single larger PAs and granting these new larger areas National Park statuses, or by improving the connectivity of smaller PAs, as good connectivity between PAs helps maintain healthy populations of large mammals (Salvador *et al.* 2011).

Transfrontier parks are formed when two areas border each other across international boundaries (DEA 2016). Authorities responsible for the respective areas formally agree to manage the areas as one integrated unit according to a streamlined management plan (DEA 2016). The authorities also undertake to remove all human barriers within the transfrontier park so that animals can roam freely (DEA 2016). Transfrontier parks provide greater opportunities for protecting fragile environments and generating greater funds, however, they also raise issues of sovereignty of national governments, create complexity in governance processes and can lead to the needs of rural communities being sacrificed (Bhatasara *et al.* 2013). If local clusters of smaller PAs in North America were to merge to form single, larger PAs, as suggested above, it is possible that similar issues would arise and conflicts between states would need to be reconciled.

In Chapter Two, Australia was identified as a region of relatively low TM species attractiveness, compared to other regions of the world (Figures 2.8 & 2.9). I suggested that this finding may be an artefact of the sources used for deriving TM species, and PA, attractiveness. I defined TM species, and PA, attractiveness as the number of times, or number of sources, that mentioned a specific TM species, or PA, respectively. The majority of sources used were published by UK based companies (Table 2.3). Assuming that their target audiences are also UK based, the time and financial cost associated with travelling from the UK to more remote destinations may help explain why TM species, and PAs, in Australia were not mentioned as many times in, or by as many of, the sources, and were subsequently allocated relatively low TM species and PA attractiveness values. Furthermore, WB-tourists are often drawn to Australia and other island countries by the existence of high levels of endemism and non-TM species (Valentine & Birtles 2008; Home *et al.* 2009). In this study I focused on WB-tourists with TM species viewing preferences, however, future studies should consider a greater number and diversity of taxonomic groups and

natural features in their definitions of wildlife attractiveness, so that areas with high WBT potential can be highlighted for WB-tourists with broader wildlife viewing preferences.

3.4.3 Protected Areas with High Wildlife-Based Tourism Potential

PAs in upper Amazonia and sub-Saharan Africa, specifically the eastern and southern African savannahs, received the highest predicted PA-LOS (Figures 3.10A & 3.10B) and PA-IOA (Figures 3.11A & 3.11B) values. The highest abundance of 'false positive WBT destinations', defined as PAs that were selected as WBT destinations by the best fitting model of PA-LOS but were not mentioned by the sources, are also found in these regions (Figures 3.12A & 3.12B).

The Amazon is one of the richest biodiversity hotspots on Earth (Myers *et al.* 2000). It is home to more species of plants and animals than any other terrestrial ecosystem (Salvador *et al.* 2011), with western Amazonia hosting the highest TM species biodiversity in the Amazon basin (Tuomisto *et al.* 1995; Voss & Emmons 1996; Peres 1999; Gascon *et al.* 2000). WBT has been presented as one of the few feasible means of generating incomes for local Amazonian populations without compromising the conservation of their ecosystems (Yu *et al*. 1997; Gössling 1999; Hearne & Santos 2005), as it can tie the conservation of Amazonian forests in with the development of locally owned WBT operations (Salvador *et al.* 2011). However, encouraging WB-tourists to visit biologically sensitive habitats, such as the Amazon, in search of vulnerable species may be detrimental to the wildlife species and habitats in which they reside (Gurung *et al.* 1994; Noss *et al.* 1996; Nepal 2000; Reynolds & Braithewaite 2001; Sekercioglu 2002; Müllner *et al.* 2004; Steven *et al.* 2011); especially as environmental awareness in Amazonia remains low, which threatens uncontrolled tourism in the region (INTOSAI 2015). To help minimise the stress and

disturbance caused by WB-tourists to the environment, education programs, that improve knowledge and awareness of environmental issues, should be implemented (Burns 2003), and exposure of fauna to large numbers of WB-tourists should be carefully regulated (Schenck 1999; Karp & Root 2009).

At present, the impacts of WB-tourists on wildlife are being monitored in approximately 50% of PAs in developed countries and in less than 35% of PAs in developing countries (Giongo *et al.* 1993). Continuous monitoring allows for adaptive management i.e. if management objectives are not being met, management actions can be adjusted (Eagles *et al*. 2002; Karp & Root 2009). Continuous monitoring is especially important for WBT because of the dynamic nature of both wildlife and WB-tourists. Significant improvements in the planning, management and monitoring of WBT sites are required, to help minimise the negative impacts of WB-tourists on the environment and to ensure WBT makes a net positive contribution to conservation (Tapper 2006).

Previous studies have predicted that the WBT industry has the potential to grow considerably faster in Africa than in the rest of the world (Ashley & Elliot 2003). However, many PAs in Africa remain underfunded, lack infrastructure and amenities which forms a deterrent for international tourists, and only exist as 'paper parks', such that the conservation laws to which they are bound only exist on paper, or are insufficient to stop further degradation (Khadaroo & Seetanah 2008; Wilkie & Carpenter 1999). Greater investments in the management of 'paper parks' and in the development of infrastructure and amenities for WBT in sub-Saharan Africa are required, to help facilitate growth of new WBT operations in the region.

Local communities in developing countries, where opportunities for WBT are often greatest, rarely possess the skill set demanded by tourism jobs, such as knowledge

of language beyond the local dialect, or the capital required to start-up businesses in the tourism industry (Timothy 2002). Instead, tourist operations in these regions tend to be owned and managed by non-locals (Burns & Sofield 2001). When employees are locally recruited, they often occupy more menial positions and are paid less than non-local employees (Mvula 2001; Burns 2003). In Kenya, for example, PAs with high visitation rates and high revenues show high levels of poverty in neighbouring communities (Okello *et al.* 2009; Homewood *et al*. 2009). It has been estimated that less than 2% of the US$31 million generated by tourism in the Serengeti, between 1993 and 2003, stayed with local communities (Kideghesho *et al.* 2006).

The long-term sustainability of WBT operations depends on their ability to improve the livelihoods of local communities and on the attitudes of local residents towards conservation (Wahab & Pigram 1997; Bookbinder *et al.* 1998; Walpole & Goodwin 2000; Kiss 2004; Coria & Calfucura 2012; Liu *et al.* 2012). Helping local communities earn a sustainable income from WBT could (1) help minimise their economic dependence on less sustainable activities (such as agriculture, hunting and logging) that exploit natural resources directly and are more damaging to biodiversity than WBT, and (2) could provide greater incentive for locals to engage with conservation efforts, making them more likely to protect, and potentially invest future resources into, their land (Prescott-Allen & Prescott-Allen 1996; Adams & Infield 2003; Langholz 1999; Jones & Young 2004).

3.4.4 Limitations and Recommendations

In this study, I estimated PA attractiveness using a range of global WBT guide books, travel brochures and online resources (Table 2.3). I assumed that the number of sources that mentioned a PA was indicative of its attractiveness to WB-tourists. Visitation rate figures of WB-tourists to PAs worldwide are required to validate these

estimates of PA attractiveness. Unfortunately, such data are not yet available, so this validation was beyond the scope of my project. However, I used available visitation rates to determine whether (or not) the best fitting model of PA-IOA could be used to estimate the number of people that visit PAs worldwide. No correlation was found between visitation rates and actual, or predicted, PA-IOA values, suggesting that PA-IOA is a poor measure of PA visitation rates and/or that the features of PAs that make them attractive to general tourists differ from the features that make them attractive to WB-tourists. This is in accordance with previous studies that suggest motivations for how and where to recreate vary between different types of tourists (Wood *et al.* 2013). 'Backpackers', for example, are often attracted to regions 'off the beaten track' that are void of tourism infrastructure, whilst high income tourists are more prevalent in areas where they can enjoy greater exclusivity (Walker *et al.* 1998). Local tourists are often attracted to PAs with greater accessibility and local amenities, such as shops and markets, whilst the quality of accommodation is a more important consideration for international tourists, when deciding whether (or not) to visit a specific PA (Balmford *et al*. 2014).

I estimated wildlife attractiveness using predicted PA species lists, generated by overlaying PA and TM species polygons. The mean Jaccard similarity coefficient (0.619 ± 0.157 standard deviations) suggests that the PA polygon overlay method is an acceptable method for estimating wildlife attractiveness of PAs worldwide (Figure 3.1). However, future studies should use knowledge of TM species' habitat preferences, the distribution of remaining suitable habitat, and species' elevation limitations to refine TM species' mapped ranges and improve estimates of which TM species are present in each PA worldwide (Somveille 2013). I estimated PA accessibility by measuring the shortest straight-line distance from the PA polygon perimeter to the x-y coordinates of its closest international airport. However, accessibility also depends on the availability and quality of road infrastructure

between the airport and PA, as well as the time, distance and financial costs incurred by international WB-tourists, from their countries of origin to each PA's closest international airport. Future studies could improve estimates of accessibility using journey time and distance information from Google Maps (available at: https://www.google.co.uk/maps), from starting points in each of the principal regions whose inhabitants participate in WBT, to each PA.

Finally, I excluded PAs with only point, rather than polygon, data available. However, PAs with point records are heavily biased toward the representation of smaller PAs (IUCN 2016). This may have reduced the predicting power of my models, and resulted in biases in my results.

3.5 CONCLUSION

In this Chapter, I built a modelling framework to predict which features of PAs make them attractive to WB-tourists. The model predicts larger, less remote PAs, with higher wildlife attractiveness values are more attractive to WB-tourists than smaller, more remote PAs, with lower wildlife attractiveness values. I used the model to highlight PAs with high WBT potential that are currently underexploited. The model highlighted PAs in upper Amazonia and sub-Saharan Africa. New WBT operations in these regions could (1) have significant socioeconomic benefits for local communities, (2) help generate substantial revenue for conservation, which could be used to help manage and protect the PA's species and habitats, and (3) help prevent the over-utilisation of 'popular' WBT sites, that have already been heavily exploited (Dharmaratne *et al*. 2000; Lindsey *et al*. 2007; Bayliss *et al*. 2014). However, new WBT enterprises must strike a balance between satisfying tourist demand and minimising the stress and disturbance caused to the environment by WB-tourists, to ensure WBT has a net positive impact on the PA's biota. It is uncertain how much local communities benefit from WBT (Blangy & Mehta 2006), and there is concern that 'revenues from tourist income… [are] not being earmarked for protected area management' (IUCN 2003). Future studies are required to determine how much revenue WBT is providing to PAs, and what percentage is being earmarked for local communities and conservation (Stronza 2008).

Chapter Four: Conclusion

4.1 Thesis Summary

In this thesis, I identified (1) species traits and (2) features of protected areas (PAs) that make them attractive to wildlife-based (WB) tourists, and highlighted regions with high wildlife-based tourism (WBT) potential that are currently underexploited.

In Chapter Two, I explored the traits that make terrestrial mammal (TM) species more (or less) attractive to WB-tourists. I built a modelling framework to predict TM species attractiveness, based on a range of species traits and characteristics. The model predicted that larger, increasingly threatened TM species are more attractive to WB-tourists than smaller, more common TM species. There is concern that the dependence of WBT operations on large, threatened species may reduce funds available for wider biodiversity conservation and limit the extent to which areas lacking these species could benefit from WBT (Kerley *et al.* 2003; Andelman & Fagan 2000; Lindsey *et al.* 2007; Okello *et al*. 2008). Changes in marketing, and improvements in public education, could help increase knowledge and awareness of a wider range of species, directing attention away from large, threatened TM species, and towards other taxonomic groups.

In Chapter Three, I explored the factors that lead to specific PAs being attractive to WB-tourists. I built a modelling framework to predict PA attractiveness, based on a range of socioeconomic and biogeographical variables. The model predicted that larger, less remote PAs, with higher wildlife attractiveness values are more attractive to WB-tourists than smaller, more remote PAs, with lower wildlife attractiveness values. This finding calls for greater investment in wildlife conservation, as future loss

of large, threatened TM species from a PA may reduce the area's potential as a WBT destination, and for larger areas to be protected, to increase their WBT potential. Protecting larger areas could have positive implications for conservation as the number and rate of species extinctions in PAs declines with increases in PA size (Brashares *et al.* 2001; Newmark 1987; Rivard *et al.* 2000; Friedlander *et al.* 2007; Gurd *et al*. 2001).

PAs in upper Amazonia and sub-Saharan Africa were identified as areas with high WBT potential that are currently underexploited. New WBT operations in these regions could help generate substantial revenue for both local economies and conservation (Dharmaratne *et al*. 2000; Lindsey *et al*. 2007; Bayliss *et al*. 2014). However, new WBT operations must focus on minimising their negative environmental and social impacts, and maximising their contribution to local communities and conservation, by supporting social and economic development, and by assisting the long-term survival of species and the habitats in which they reside, respectively (Wunder 2000; Blangy & Mehta 2006; Stronza & Pegas 2008).

Encouraging WB-tourists to visit biologically sensitive habitats, such as the Amazon, in search of vulnerable species may be detrimental to the species and habitats in which they reside (Gurung *et al.* 1994; Noss *et al.* 1996; Nepal 2000; Reynolds & Braithewaite 2001; Sekercioglu 2002; Müllner *et al.* 2004; Steven *et al.* 2011). WBT operations must strike a balance between satisfying tourist demand and minimising the stress and disturbance caused to the environment by WB-tourists, to ensure that there is a net positive impact on the PAs biota. Greater rewards for tour operators that support conservation, and better support for landowners who wish to develop responsible WBT operations, may help enhance the contributions of WBT to conservation (Higginbottom *et al.* 2001).

Tour operators must also respect local cultures and seek to improve the livelihoods of local people (Wunder 2000; Blangy & Mehta 2006; Stronza & Pegas 2008). Ensuring local communities earn sustainable incomes from WBT helps reduce their economic dependence on less sustainable activities, such as agriculture, hunting and logging, which exploit natural resources directly and are more damaging to biodiversity (Langholz 1999; Jones & Young, 2004). Furthermore, it can provide locals with greater incentive to engage with conservation efforts, making them more likely to protect, and potentially invest future resources into, their land (Prescott-Allen & Prescott-Allen 1996; Adams & Infield 2002). There is a need for strong, coordinated government leadership, involving all stakeholders, to ensure both social and economic benefits are received locally from WBT and best-practice codes and guidelines are implemented (Schevyens 1999; Stronza & Pegas 2008).

4.2 Thesis Applications

The EU Blue Flag Programme for beaches and marinas promotes sustainable development in coastal areas through high water quality standards, safety standards, environmental management standards and environmental education (FEE 2016). It is used to endorse high quality assets, for example, beaches are identified by a particular symbol when they have been evaluated as clean and safe (Deng *et al*. 2002). Similarly, the IUCN Green List aims to improve the contribution that PAs make to sustainable development by *"encouraging PAs to measure, improve and maintain their performance through globally consistent criteria that benchmark good governance, sound design and planning, effective management, and successful conservation outcomes" (IUCN 2016).* The IUCN Green List is also used to endorse high quality assets, for example, PAs receive a 'Green List' certificate if they achieve the Green List Standards (IUCN 2016).

PA management costs increase as visitation rates increase (Moore & Carter 1991). Park entrance fees and commercial operator permit fees need to increase accordingly to help park managers recover their costs (Moore & Carter 1991). In Chapter Three, I built a modelling framework to predict PA attractiveness, which I used to allocate attractiveness values to PAs worldwide. Similar models could be used to endorse high quality PAs, in terms of their assemblage of WBT-attractant species, enabling WB-tourists to anticipate what to expect from a PA by virtue of its rating and/or by park managers to price PAs according to PA attractiveness or visitation rates (Berkley 1998). There is a risk that this system might increase visitation rates to larger, well-established PAs and reduce visitation rates to PAs that are more in need of the income, consequently, this system would require careful management and monitoring.

4.3 Future Directions

4.3.1 Cost-benefit Analyses

Transport (particularly air traffic) is responsible for the majority of negative environmental impacts associated with international WBT (Gössling *et al.* 2002). It has been estimated that more than 97% of a WB-tourist's energy footprint is a result of air travel, and that the carbon dioxide emissions of a relatively short one-way international flight from Australia to New Zealand is approximately equivalent to the total transport-related carbon dioxide emissions of a hypothetical 20-day self-drive eco-tour in New Zealand (Simmons & Becken 2004). Even if local-level WBT is considered sustainable, and presents minimal threats to local ecosystems, international WBT involving long-haul flights cannot be viewed in the same light (Gossling *et al.* 2002).

With an increased focus on reducing individual carbon footprints, WB-tourists, who wish to visit pristine sites, yet avoid negative environmental impacts, face a dilemma in terms of which sites to visit. In this study, I have identified features of PAs that make them attractive to WBT. However, future studies could use Ecological Footprint (EF) analysis to highlight priority sites for WBT based on cost-benefit statistics, that maximise attraction, yet have minimal carbon and/or financial costs. EF analysis is more commonly used to estimate the demands upon the biological productivity and assimilative capacity of the biosphere imposed by a given human population over a period of time (Chambers *et al.* 2000). Typically, calculations account for the use of energy, foodstuffs, raw materials and water, and also capture transport-related impacts, the production of wastes (including carbon dioxide from the burning of fossil fuels), and the loss of productive land associated with buildings, roads and other aspects of the built environment (Chambers *et al.* 2000). However, EF analysis can also be used as an indicator of sustainable tourism (Hunter and Shaw 2002). EF allows quantitative comparisons between different components of a tourism adventure, such as transit zone and destination area footprints, and can provide an indication of the overall ecological impact of tourism on global biological resources.

4.3.2 Impacts of Climate Change on Wildlife-based Tourism

Over the past ten years, there has been an upsurge of studies on the complex interconnections between nature-based tourism (NBT) and climate change (Stronza & Pegas 2008; Scott *et al.* 2007). Climate impacts the resources that define the nature and quality of natural environments and directly affects NBT by limiting when and where specific recreational activities can occur, such as hiking, swimming and camping (Scott *et al.* 2007).

According to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), confidence is very high that climate change will result in: increased temperatures, more severe and more frequent heatwaves, significant sea-level rises and increased intensity, and perhaps frequency, of extreme weather events, including tropical cyclonic activity, extreme drought, heavy precipitation events and flooding (IPCC 2014). All of these predicted changes are likely to have significant effects on NBT in particular regions and localities. For example, in western North America, glaciers are important tourist attractions for mountain parks, however, they have been retreating over the past century and are projected to continue to do so under future climate change (Scott *et al.* 2007).

Species' distributions and abundances are strongly influenced by climate (Walther *et al.* 2002). Many species are responding to the warming global climates by shifting their distributions to higher latitudes and/or altitudes (Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003; IUCN 2001), causing their range boundaries to shift both into, and out of, existing PAs (Hannah *et al.* 2007). Consequently, the current presence of a species in a PA is not a guarantee of its future persistence. If an attractive species, such as a lion (*Panthera leo*) or tiger (*Panthera tigris*), is unable to persist in a PA in the future, due to the absence of climatically suitable habitat, this may affect the presence/absence of other species in the PA, as well as PA's visitor numbers and revenues (Palmer *et al*. 2008). Equally, changing species' ranges may create new opportunities for WBT in PAs that are currently not target sites for WBT due to a present lack of WBT-attractant species (Peters & Darling 1985). It is important to understand how the changing distribution of species might affect WBT in the future. Future studies should consider how PA attractiveness and visitation rates might change under projections of future distributions of species, given climate change predictions. Such findings could be used to highlight areas of high future WBT potential, resulting from climate-induced changes in species assemblages. This

could have significant geopolitical consequences, particularly in the case of developing countries that currently rely heavily on WBT for sustaining their economies.

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